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PLANT DISEASE FUNGI



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TORONTO

PLANT DISEASE FUNGI

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PREFACE

The aim of this book is to present the more important facts concerning the morphology and taxonomy of the fungous parasites that affect plants of importance in the continental United States, with some discussion, also, of the more significant facts of morbid histology. Technical description of each division, order, family, genus and species, when important, is given unless the essential characters are to be clearly inferred from preceding keys or text. In order to avoid duplication of the subject matter of "Diseases of Economic Plants" gross descriptions of diseased hosts are omitted from this volume.

Bibliographic citations given either in "Diseases of Economic Plants" or in "The Fungi which cause Plant Disease," in general, are not repeated here and the student is referred to these two texts for additional references to literature. The citations herein given refer to articles either more recent than those of the previous work or are advisable owing to a different viewpoint in the present book. Effort has been made to present at least one illustration of each genus of importance. The keys, for the most part, are abbreviated or otherwise modified from those given in "The Fungi which cause Plant Disease." All keys are abridged by the omission of genera or larger groups whose representatives are of minor importance.

The author wishes to express thanks for suggestions and criticism of the manuscript to F. W. Tanner who read the portion on Bacteria; G. P. Clinton, Ustilaginales; E. C. Stakman, and H. R. Rosen, Uredinales; C. L. Shear, the anthracnose fungi; E. A. Burt, certain Basidiomycetes; C. D. Sherbakoff, the genera *Fusarium* and *Nectria*; and to B. B. Higgins for kindly reading critically the entire book in proof.

F. L. STEVENS.

URBANA, Illinois.
March, 1925.

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PLANT DISEASE FUNGI

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INTRODUCTION

A large percentage of all plant diseases is caused by fungi. Fungi are devoid of chlorophyll and while transpiration, respiration, and true assimilation are the same as with the green plants, photosynthesis or starch manufacture cannot be accomplished by them. Sunlight being thus unnecessary they can live in the dark as well as the light. Having no ability to elaborate their own foods from inorganic matter these organisms are limited to such nutriment as they can obtain from plants or animals which have elaborated it; that is, they must have organic foods for their sustenance.

The fungi have acquired various food habits and adapted themselves to different methods of nutrition. Some are nearly omnivorous and can subsist upon almost any decaying tissue or upon soils or solutions rich with organic débris. Others thrive only upon special substances, as for example, some particular plant or animal, **the host**, perhaps only upon some particular part of that plant or animal. The organisms that prey upon living things are called **parasites**. Those living upon dead things are **saprophytes**. No hard and fast line can be drawn between these two classes. An organism which is usually a saprophyte may live upon a dead member of some plant, gradually encroach upon the still living part and thus become partially a parasite. Again there are times in the history of a plant when life ebbs so low that it is difficult to tell the living from the dead. The pulp of the apple when ripe, a resting seed, the cells of the potato tuber in winter, are undoubtedly alive, yet their activity is so slight that many organisms can gain a foothold upon these stages of the plant that cannot do so at more vigorous periods of its existence.

No discussion of the general metabolic processes of the fungi is here necessary further than to indicate that among the products of their activity there are various excretions and secretions, which

bear important relation to parasitism. Thus certain fungi growing in artificial culture produce **enzymes** or **organic ferments** capable of softening and dissolving cellulose, also **toxins**, poisons which are capable of killing the cells of the host plant. Such enzymes and toxins are numerous and their bearing upon parasitism is obvious. They enable the parasite to kill adjacent cells of the host and then to effect an entrance through the cell walls to the protoplasm and other nutrients contained within the cell.

The presence of the parasite, or secretions produced by it, often calls forth abnormal growth responses from the host. These take very diverse forms, either the undergrowth or overgrowth, hypertrophy, of single cells or tissues, or even the excessive development of large plant parts as in the case of the witches' brooms, and the "double flowering" of the dewberry.

Study of the fungi present in diseased tissues and of their relation to these tissues is of great importance as an aid in diagnosis.

If no fungi are found in sufficient abundance to account for disease, after careful search in all parts of the plant, it may tentatively be assumed (flowering plants and animal parasites being similarly excluded) that the disease is non-parasitic in origin. If fungi are found their morphology must be ascertained and their taxonomic position determined in order to render diagnosis certain and to make available the literature pertaining to the disease. It is the purpose of the following pages by keys and descriptions to aid the student in such studies.

The principal, non-flowering, vegetable parasites which cause plant diseases belong to three divisions: the **Slime Molds (Myxomycetes)**; the **Bacteria (Schizomycetes)**; and the **True Fungi (Eumycetes including the Phycomycetes)**. The term **fungi**, in the broad sense, is often used to include all three of these divisions.

Key to the **three Divisions** important as plant parasites:

Vegetative body a multinucleate, naked plasmodium

Division I. Myxomycetes, p. 3.

Vegetative body a single, walled cell, reproduction by fission (by conidia in a few forms).....

Division II. Schizomycetes, p. 9.

Not as above: vegetative body usually filamentous, reproduction by various means.....

Division III. Eumycetes, p. 50.

DIVISION I

MYCETOZOA, MYXOMYCETES, PLASMODIOPHORACEÆ ^{1, 2} (p. 2)

The distinctive character of the members of this division is that the vegetative plant body as it approaches maturity consists of a mass of naked protoplasm, the **plasmodium**, formed by the coalescence of numerous swarm cells, each unwallled. The plasmodium eventually gives rise to walled spores; they in turn germinate, producing amœboid swarm cells, which soon become flagellated. These swarm cells multiply by division and ultimately revert to the amœboid condition and coalesce, bringing about a return to the plasmodial stage.

The fungi herein considered may be separated, on the purely artificial character of parasitism, into two groups.

Parasitic.....	Plasmodiophoraceæ , p. 3.
Saprophytic.....	Mycetozoa , p. 7.

Plasmodiophoraceæ ^{2, 3}

Intracellular parasites, vegetative stage plasmodial; spores formed by the simultaneous breaking up of the plasmodium into an indefinite number of independent cells.

Since the protoplasm of the parasite rests within the protoplasm of the host this constitutes parasitism of the strictest type.

KEY TO GENERA OF **Plasmodiophoraceæ**

- Spores free, spherical..... 1. **Plasmodiophora**, p. 4.
- Spores united into groups
 - Spores in groups of more than four
 - Spores forming a spongy spore-ball..... 2. **Spongospora**, p. 5.
 - Spores in a cyst..... 3. **Cystospora**, p. 6.

¹ Lister, A. A monograph of the mycetozoa. British Museum of Natural History, London, 1911.

² Osborn, T. G. B. The life cycle and affinities of the Plasmodiophoraceæ. Rept. Brit. Ass. Adv. Sc. Portsmouth, 572, 1911.

³ Schwartz, E. J. The Plasmodiophoraceæ and their relationship to the Mycetozoa and the Chytrideæ. Ann. Bot. **28**: 227, 1914.

Plasmodiophora Woronin (p. 3)

This genus is parasitic in the living parenchyma of the roots of plants, plasmodia filling the cells and causing galls at the point of attack.

Only one species is of importance.

P. brassicæ Wor. is parasitic on crucifers generally and perhaps on members of other families; the Umbelliferae and cucurbits.

The parasitized cells especially, and the adjacent cells as well, are stimulated to enormous overgrowth; (**hypertrophy**) and there is also large increase in the number of cells by abnormal cell divi-

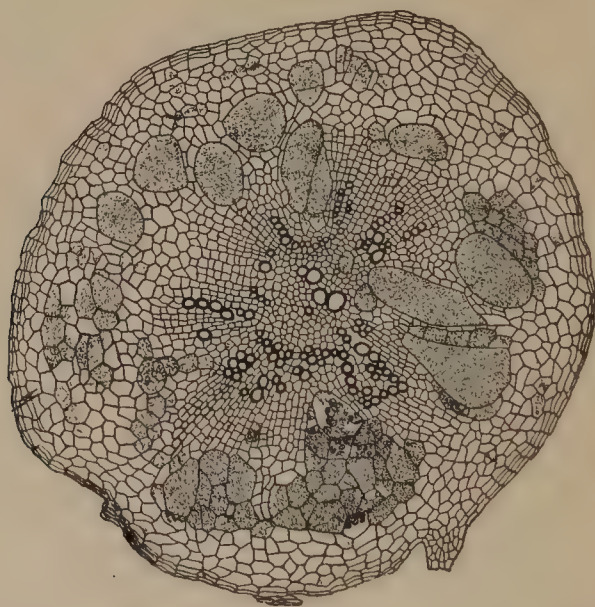


FIG. 1.—Cross-section of a root badly infected with *P. brassicæ*.
After Woronin.

sion (**hyperplasia**) resulting in the formation of galls, often very large, on the underground parts of the host.

In early stages of the disease of a cell, nuclear and cell division is not seriously affected, but in later stages both processes cease and the host nucleus degenerates.

Study of diseased sections shows that the medullary rays and cortex are abnormally thick (hypertrophy and hyperplasia) and many of their cells are parasitized. Sclerenchyma cells are suppressed by the parasite, the xylem is reduced and phloem increased

proportionately. The amount of stored starch is much less than in normal tissues.



FIG. 2.—Germination of the spores and development of the myxamebae. After Woronin.

Infection occurs through the root hairs by the single amœboid cells, and groups of diseased cells arise from repeated division of a cell after its infection. Passage of the organism from cell to cell also occurs.

In the enlarged host cells the protoplasm appears abnormally dense and fine grained. Eventually the lumen of the cell is largely occupied by the crowded, amœboid individuals, which later fuse into plasmodia, the nuclei of which enlarge and undergo simultaneous mitotic division. Still later the mass divides into uninuclear segments each of which matures to a spore 1.9–6.9 μ in diameter, covered by a thin, smooth, colorless membrane.

Spore germination may best be studied in a muck-soil filtrate, where in from five to twenty-four hours uninucleate zoöspores are produced. The zoöspores are differentiated into an inner granular, and an outer hyaline region, the hyaloplasm, which may extend to form pseudopodia, thus giving the cell an amœboid movement in addition to that due to the single long cilium.

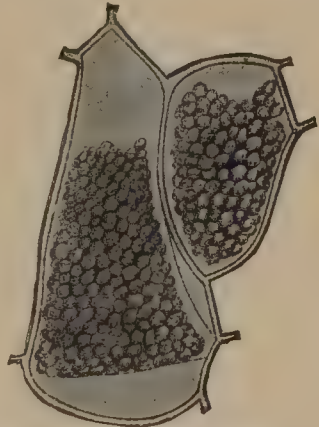


FIG. 3.—*P. brassicae*: host cell full of spores. After Lotsy.

Seedlings raised in soil inoculated with chopped roots bearing the disease become badly diseased as do also seedlings upon which infected water is poured.

Other species have been reported on hops, tomato, orchid.

***Spongospora* Brunchorst¹ (p. 3)**

S. subterranea (Wallr.) Johnson causes the powdery scab of potato tubers, also galls on the roots, stolons and stems, and galls on tomato roots.

¹ Osborne, T. G. B. *Spongospora subterranea* (Wallroth). Johnson. Ann. Bot. **25**: 271, 1911.

Infection of growing potato tubers by *S. subterranea* is accomplished not by separate amœbæ, as has previously been supposed, but through the action of a plasmodium which invades the tissue and infects a large number of cells at each point of contact.

The diseased host cells are consumed by the parasite resulting in pits or cavities. At the same time adjacent host cells are stimulated to increased growth and division. The parasite is handed down to new cells as division of parasitized cells occurs. The plasmodia

at maturity produce spores which adhere in loosely aggregated, spongy, ovoid to spherical, balls which are about $50\ \mu$ in diameter. The individual spores are about $4\ \mu$ in diameter.

Cystospora Elliott (p. 3)

This genus differs essentially from *Plasmodiophora* in that the plasmo-

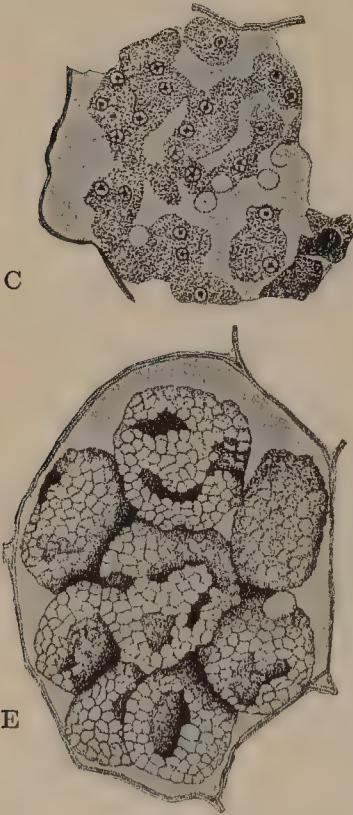


FIG. 4.—*S. subterranea*. *C*, The amœbæ are coalescing to form the plasmodium. *E*, Mature spore balls in an enlarged host cell. After Osborne.

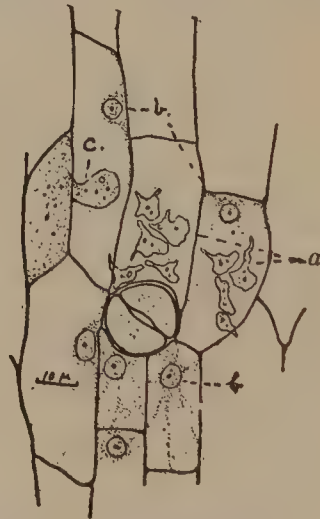


FIG. 5.—*C. batatae*. Cells of a growing-point occupied by several individuals in the amœboid stage. *a*, parasites; *b*, host cell nuclei; *c*, plasmodium invading cell. After Elliott.

dium within the host cell becomes encysted before formation of the spores, Fig. 6. Each cyst bears several hundred spores.

C. batatae (Ell. & Hals.) Elliott

This organism was originally described by Halsted under the

name *Acrocystis* as the cause of soil rot of sweet potatoes, and was later by Elliott referred to the Plasmodiophoraceæ. Elliott's description is essentially as follows:

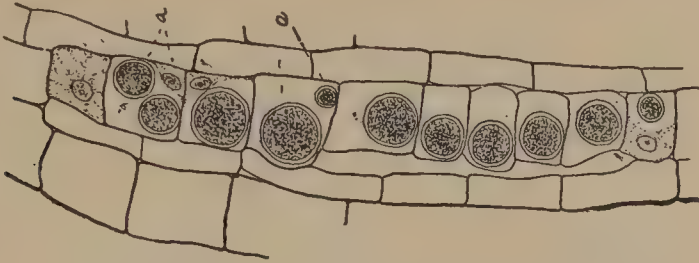


FIG. 6.—*C. batatae*. Row of host cells occupied by cysts of the plasmodium. *a*, host cells containing two cysts. After Elliott.

In large, shallow pits a plasmodium is present, the host cells invaded, and the contents dissolved. In the root tips swarm spores invade the host cells, pass to the amœboid stage, multiply rapidly, then form a plasmodium which encysts. Inside of the cyst hundreds of swarm spores develop and later emerge to penetrate other cells.



FIG. 7.—*Physarum cinereum*. After Lister.

Mycetozoa (p. 3)

This group comprises some forty-nine genera and about two hundred and fifty species of great variety and beauty. The plasmodium, which varies from a millimeter or less to several deci-

meters in diameter, produces either flat, encrusted masses of spores, *æthalia*, or develops spores in sporangia which show some superficial resemblance to very small puffballs, Fig. 7. The interior of the sporangium is often permeated by a threadlike structure, the *capillitium*. They are not parasites but occasionally injure plants by overgrowing them.

The species most often found so doing is *Physarum cinereum* Pers. which forms its tiny, sessile, gray sporangia in great numbers on living plants, often smothering them. The peridium is lime-charged, as are also the nodes of the capillitium. The spores are brown or violet, and warty. *Physarum gyrosum* Rost. and *Musilago spongiosa* Morgan are credited with similar injury.

DIVISION II

BACTERIA, SCHIZOMYCETES^{1, 2} (p. 2)

Bacteria are extremely minute, unicellular organisms, which in outline present three primary forms each of great simplicity, namely the spheres (**cocci**), the straight rods (**bacteria**), the curved rods (**spirilla**).

In addition to these forms which comprise the vast majority of known species of bacteria there are also bacteria consisting of filamentous bodies, either simple or branched, attached or free. In both structure and physiology bacteria are allied to the vegetable kingdom and in it most closely to the blue green algæ.

Bacteria are inconceivably small. Most of the spherical bacteria fall within the limits of from 0.5 to 1.5 μ in diameter. Among the rod and curved bacteria the length in most species is between 1 and 1.5 μ , the diameter between 0.5 and 1 μ .

Among the largest species is *B. megatherium*, 2.5 x 10 μ ; *Clostridium butyricum*, 3 x 10 μ ; and *Spirillum volutans*, 13 to 50 μ long. Among the smallest are *Spirillum parvum* 0.1–0.3 μ in diameter and *Pseudomonas indigofera* 0.06 x 0.18 μ .

It is practically impossible to conceive these dimensions. An illustration may aid the imagination. The paper on which these words are printed is about 87.5 μ thick. It would therefore take

about 200 bacteria of ordinary size or 400 moderately small or 20 very large ones placed end to end to equal in length the thickness of this paper. It would take 1571 ordinary bacteria (1 x 2 μ) end to end to reach around the circumference of a dot 1 mm. in diameter

FIG. 9.—This dot is 1 mm. in diameter.



FIG. 8.—The three type forms of bacteria; a, spheres; b, rods; c, spirals. After Conn.

¹ Smith, E. F. Bacterial diseases of plants. W. B. Saunders Co., Philadelphia, 1920.

² Bacteria in relation to plant disease, Vols. 1–2–3. Carnegie Institution, Washington, 1905.

(Fig. 9), 500 to equal its diameter, 392,700 placed side by side or 785,400 if placed on end to cover its area, and about 500,000,000 to fill a cube the edge of which is 1 millimeter, making no allowance for lost space of the interstices. Considerably more than 500,000,000,000 bacteria of this size would find room enough to move about in a space of one cubic centimeter.

The typical mode of increase in the eubacteria is by **fission** or **direct division** of one cell, the **mother cell**, into two, the **daughter cells**. Fig. 10. The rapidity with which fission can proceed depends, of course, upon conditions of environment, ranging from no growth at all, due to cold, lack of nutriment, presence of inhibit-

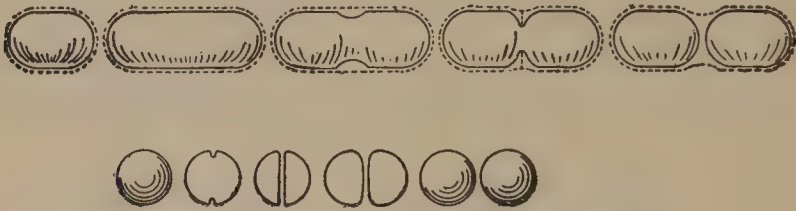


FIG. 10.—Diagram illustrating the fission of bacteria, bacilli and cocci.
After Novy.

ing substance, to a maximum that varies with the species. For bacteria in general in very favorable environment, with proper temperature and abundance of food, from 20 to 40 minutes may be reckoned as a generation. In 24 hours, with the divisions once each hour, the progeny of one germ will be 16,777,216; with divisions each 30 minutes it will be $(16,777,216)^2$.

If cell division be in one direction only and the resulting daughter cells remain undisturbed, a thread-like row results. If cell division be in two planes, and the resulting cells adhere in groups, tablets of 8, 16, and 64 will occur frequently. If the division be in three planes and their cells adhere, packets result.

The structure of the bacterial cell. The most enduring portion of the vegetative cell is the cell wall. This is surrounded by a layer, the **capsule** and bears the **flagella**, the organs of locomotion. The number of the flagella and their position varies in different species; some species have none, some one, two, or many. They may be at the ends, **polar**, or scattered over the whole surface, **diffuse** or **peritrichiate**. Within the wall is the **protoplast** consisting of a peripheral layer, inner strands, imbedded granules and **vacuoles** bearing cell sap. The existence of a nucleus comparable to that in higher plants is a much controverted point.

Spores: Typically a bacterial spore consists of a highly refractive, ovoid, walled body within the mother cell. They are most frequently met among the rod forms, and are rare among the spirilla and cocci. None are known among the important plant pathogens. This body possesses high resistance to ordinary stains, a great tenacity against decolorizing if it be once stained, a higher resistance against adverse temperatures and adverse conditions generally than do vegetative cells, and finally the ability to germinate and thus aid in perpetuating the species. While the absolute number of bacterial species that form spores is large, comparatively they are few.

In the simplest cases of spore formation, the protoplasm becomes more dense in some part of the mother cell, the remaining protoplasm of the



FIG. 11.—Spores of bacteria showing their position within the cell. After Frost & Mc-Campbell.



FIG. 12.—Spore formation in bacteria. After Fischer.

cell is drawn around the denser mass, and the whole resulting dense region becomes enclosed within a special wall. Usually in this process nearly all the protoplasm of the mother cell, the **sporangium**, is used. The mother cells during spore formation may remain of the normal vegetative size and shape; they may take on (*B. subtilis*) or abandon (*B. megatherium*) the habit of thread formation. Bacteria of many species become swollen at the point where the spore develops, Figs. 11 and 13; be this in one end (*Vibrio rugula*) or in the middle (*B. inflatus*). The swelling at the end is very common, giving rise to the peculiar and characteristic form known as “nail head” or “drum stick” bacteria. In nearly all species of the Eubacteria the spores are solitary.

There are three modes of **spore germination**. The most common, **polar germination**, consists in a rupture of one pole of the spore and the development of a normal vegetative cell through the opening. The second mode, **equatorial**, Fig. 13, consists in a rupture in the side instead of the end of the spore. The third mode, **absorp-**

tion, consists in a direct development of the whole spore into a vegetative cell. In suitable environment germination may occur immediately after formation; if conditions be unsuitable it may be delayed for many years.

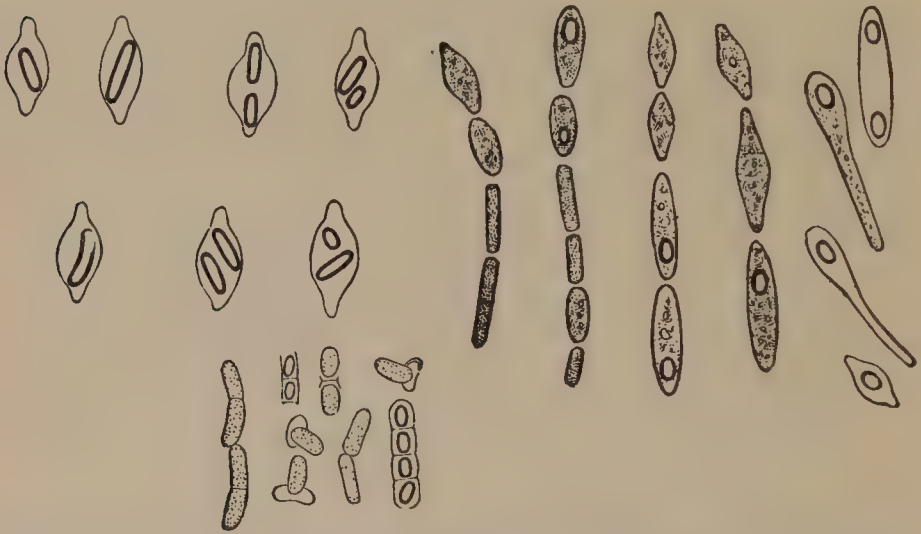


FIG. 13.—Spores of bacteria, showing bispored cells, spore formation and spore germination. After Prazmowski, de Bary and Koch.

Under certain conditions most bacteria undergo abnormal changes in form, becoming elongated, branched, swollen, bulged, curved, or variously, usually irregularly, distorted. Such are termed **involution forms**. They are, in most cases, due to unfavorable conditions of temperature and nutriment, and the bacteria resume their normal form when again in normal environment.

The branched forms found in root tubercles, after the period of luxuriant growth has passed, and the branched thread-like growth of the bacterium of human tuberculosis upon artificial media, are by many regarded as involution forms.

Bacteria were discovered by **Loewenhoeck** in 1683. That they do not originate spontaneously was shown by **Pasteur** in 1860–4. The first disease producing bacteria were recognized in anthrax by **Pollander & Davaine** in 1849; and the first definite proof that bacteria actually cause animal disease was made by **Koch** with anthrax in 1875–1878. The first plant disease definitely to be ascribed to bacteria was the pear blight by **Burrill** in 1879. The

invention of the cotton plug, Schroeder & Dusch, 1853, the gelatine method of plating for the isolation of species, Koch, 1881, and the use of stains, Weigert, 1875, were practically necessary prerequisites to any considerable advance in bacteriology. For long it was contended, especially by European bacteriologists, that bacteria do not cause plant diseases but most convincing proof to the contrary was adduced by E. F. Smith.

Entrance to the host plant is made in various ways, very often through wounds, particularly wounds caused by insects, through roots, stomata, water pores, through delicate tissues as blossoms, etc. Once in the tissue, bacteria may migrate rapidly by means of the vessels, intercellular spaces or more slowly through cavities dissolved by the aid of enzymes.

Bacteria are disseminated by wind and water, which may carry them to great distances, also by tools, hoofs of animals, shoes of man and similar means; they are in some instances conveyed from plant to plant by insects., e. g. *Bacillus tracheiphilus* on Cucurbits. Though bacteria parasitic on plants are not spore-bearing they may persist in virulent form in soil for long periods.

Classification. Several systems of classification and nomenclature are now in use in America. The system of Migula, proposed in 1894, was for years extensively employed by plant pathologists. In 1905 E. F. Smith made suggestions, since then to some extent followed, regarding the names to be used for certain genera. In 1920 the nomenclature committee of the Society of American Bacteriologists made radical changes both in system and nomenclature.

The System of Migula, in so far as it applies to important plant pathogens, and adding the Actinomycetales, is given below. Following this are given the names that would be employed for these genera if the other systems referred to were used.

The system of Migula will be used throughout this book.

SCHIZOMYCETES (p. 2)

Fission plants, without phycochrome, dividing in one, two or three directions of space. Reproduction by vegetative multiplication. Resting stages, endospores, exist in many species; motility by means of flagella in many genera.

KEY TO ORDERS, FAMILIES, AND GENERA OF **Schizomycetes**

Cells without sulphur or bacterio-purpurein, not filamentous, not branched. . . .	Eubacteriales.
Cells in free condition gobular; in division somewhat elliptical.	Coccaceæ.
Nonflagellate; division in two directions.	1. Micrococcus , p. 18.
Cells long or short, cylindrical, straight, division in one direction.	Bacteriaceæ.
Nonflagellate.	2. Bacterium , p. 18.
Flagellate	
Flagella diffuse.	3. Bacillus , p. 40.
Flagella polar.	4. Pseudomonas , p. 21
Cells filamentous, often branched.	Actinomycetales
Conidia present.	Actinomycetaceæ
Mycelium much branched and breaking into segments that function as conidia	5. Actinomyces , p. 48.

The species of the two other families of these orders, and of the two other orders of the Migula system, some 25 genera in all, are, so far as is known, unimportant in their relation to plant disease. All of the known bacterial plant pathogens belong to one or other of the first two families of the Eubacteriales or to the genus *Actinomyces*.

The specific characters of bacteria are chiefly chemical or physiological and rest in the relation of the forms to oxygen, gelatine liquefaction, fermentation of various sugars, acid production, relation to nitrogenous compounds, chromogenesis, etc.

Following the System of E. F. Smith, *Bacterium* of the Migula system becomes *Aplanobacter*; *Pseudomonas* becomes *Bacterium*; *Micrococcus* and *Bacillus* are unchanged.

The significance of the generic names as recommended by the Committee of the Society of American Bacteriologists ¹ is shown by the following abbreviated key:

Typically filamentous; mycelium and conidia formed	Actinomyces
Typically unicellular forms	
Spherical cells; saprophytic forms; cells not in packets, not in chains; fermentative powers low; yellow pigment.	Micrococcus

¹ Winslow, C. E. A., Broadhurst, J., Buchanan, R. E., Krumwiede, C., Rogers, L. A., Smith, G. H. Final report of the committee of the Society of American Bacteriologists on characterization and classification of bacterial types. *Jour. of Bact.* 5: 191, 1920.

Straight rods

No endospores

Regularly formed rods; metabolism not involving oxidation of carbon, hydrogen or their simple compounds or the fixation of atmospheric nitrogen.

Flagella usually present, polar

Pseudomonadaceæ..... **Pseudomonas**

Flagella when present peritrichic. Bacteriaceæ

Not parasitic forms showing bipolar staining; not strict parasites growing only in the presence of hemoglobin or ascitic fluid; not water forms producing red or violet pigment.

Plant pathogens..... **Erwinia**

Not plant pathogens; Gram negative, forming H_2 as well as CO_2 if gas is produced.....

Bacterium

Endospores present..... **Bacillaceæ**

Aerobes..... **Bacillus**

Types of Bacterial Disease in Plants.

Bacteria frequently occur in plant disease as the cause of **soft rot** of large areas, as of fruits (cucumber, muskmelon), tubers (potato), leaves (lettuce, cabbage), stems and roots (carrots), or as soft rot of localized areas on fruits (drupes), or leaves (drupes, grains, bean, cotton, etc.). In nearly if not in all such cases the softening is mainly in parenchymatous tissue and is due to enzymes, produced by the bacteria, which dissolve the middle lamellæ and thus free the component cells of the tissue from each other. In the early stages of such decay the causal organism alone may be present, but in advanced stages secondary bacteria or fungi may abound. **Cankers** of bark (pear, walnut) may dry out and become hard and the wood and cambium may be invaded by the bacteria.

Another type of bacterial disease is that in which the bacteria invade the xylem, more rarely the phloëm, of the veins (cucurbits, solanaceous plants, crucifers, corn, etc.) often completely filling many ducts to great distances. Wilting and death of the plant soon follows. In advanced stages of certain of these **vascular diseases** the bacteria may pass to the parenchyma and cause soft rot.

In case of bacterial soft rot or canker, bits of diseased tissue placed in a drop of water give off clouds of bacteria, usually actively motile, plainly visible under the microscope. In many instances bacterial spots, particularly when on leaves, exhibit a translucent halo surrounding the center of disease. Such translucence is always suggestive of a bacterial trouble but is of course merely suggestive.

In case of vascular thrombosis cross section of a stem is often followed in a few moments by a viscous exudate from the severed



FIG. 14—Bacterial citrus canker enlarged and photographed by transmitted light to show translucent border. $\times 6$. The tiny white specks are oil glands. (From "Bacterial Diseases of Plants" by Erwin F. Smith, W. B. Saunders Company, Publishers).

ducts. This on microscopic examination proves to be bacterial. Thin sections of diseased vascular tissue, or cross sections of diseased stems, reveal the bacteria in the ducts or issuing in clouds from them. Observations such as these are useful in diagnosis. If bacteria in abundance are present and no fungi or other probable cause of disease is apparent the presumption is that the bacteria are the etiological factor, though proof of this can rest only on evidence from inoculation by means of pure cultures.

Another type of bacterial disease is afforded by tumor, such as the familiar crown gall, so common on Rosaceous and many other

hosts (see pp. 38, 39). In this class of diseases the bacteria are present in comparatively small numbers and are very difficult of observation.

Rathay's disease of orchard grass (see p. 21) gives still another type of disease.

Some of the more prominent of the bacterial plant pathogens are listed below with the types of disease they cause. Italics indicate that this is chiefly the kind of disease produced by the organism; other type that it is secondarily of this nature.

Vascular disease.

a. of xylem: *Bact. stewarti*, *Ps. campestris*, *juglandis*, *phaseoli*, *solanacearum*, *B. musæ*, *atrosepticus*, *phytophthorus*, *tracheiphilus*.

b. of phloëm: *Bact. michiganense*.

Soft rot of parenchyma.

a. general: *Bact. teutlium*, *Ps. campestris*, *phaseoli*, *solanacearum*, *B. carotovorus*, *atrosepticus*, *phytophthorus*.

b. local: *Bact. stizolobii*, *Ps. angulata*, *avenæ*, *lachrymans*, *maculicolum*, *malvacearum*, *pruni*.

Tumor:

a. granuloma *Ps. savastanoi*

b. teratoma *Ps. tumefaciens*.

Surface parasitism: *Bact. rathayi*.

Infection of plants by bacteria may occur either through wounds or through uninjured surfaces. Examples of the former are afforded by Solanaceous plants, often invaded through broken roots; by bacteria entering through wounds produced by insects, e. g.: *B. tracheiphilus*, etc; by *B. carotovorus* which probably always enters through wounds. Examples of infection where entrance is not made through wounds are: the infection of tender delicate parts as blossoms, the organism entering through the nectaries (*B. amylovorus*); infection through water pores (*Ps. campestris*); through the stomata (*Ps. malvacearum*, *Ps. pruni*).

The plant pathogens as yet known, with few exceptions, belong to the two genera *Pseudomonas* and *Bacillus*, between which they are about equally divided.

In the earlier days of bacteriology and to some extent in recent days, bacteria have been seen in diseased plant tissues and have been placed by their observers in one genus or another and cited as the causes of the diseases in question but without actual evidence that they cause the diseases and very often without any real

evidence as to the genus to which the bacteria belonged. It is of course usually impossible to identify such forms and they must be dropped from consideration.

Coccaceæ (p. 14)

Cells in free condition globular.

No representative of this family, parasitic upon plants, has yet been reliably recorded in America, though several species of *Micrococcus* have, on incomplete evidence, been assigned as the cause of plant disease in Europe.

Bacteriaceæ (p. 14)

Bacterium Ehrenberg (p. 14)

Aplanobacter E. F. Sm.

Cells long or short, non-flagellate, cylindrical, straight, division in one direction.

These non-motile forms, perhaps owing to their lack of power of locomotion, are comparatively rare as plant pathogens.

Bact. stewarti (E. F. Sm.) E. F. Sm.^{1, 2}

= *Pseudomonas stewarti* E. F. Sm. 1898, meaning polar flagellate.

= *Bacterium stewarti* (E. F. Sm.) E. F. Sm. 1905, meaning polar flagellate.

= *Aplanobacter stewarti* (E. F. Sm.) McC. 1918, meaning non-flagellate.

This species presents interesting complications in naming since it was first named *Pseudomonas stewarti* by Smith in 1898, following the Migula system, and by him transferred to the genus *Bacterium* in 1905 abandoning Migula's genus *Pseudomonas*. In 1918 Miss McCulloch decided that the organism is devoid of flagella and named it *Aplanobacter stewarti*. Wishing to retain the Migula system I now call it *Bacterium stewarti* though with a different morphological significance than that conveyed by Smith when he first used this binomial.

A medium size rod, 0.5–0.9 μ x 1–2 μ , with rounded ends, non-motile, viscid, aërobic. Yellow, non-liquefying; does not separate

¹ McCulloch, L. A morphological and cultural note on the organism causing Stewart's disease of sweet corn. *Phytop.* **8**: 441, 1918.

² Smith. *Bacterial Diseases of Plants*.

casein in milk. T. D. P. 10 min., 53°. Agar colonies subcircular, no gas.

The bacterial corn blight of this organism was first described by Stewart in 1897 and attributed to bacteria. The organism was originally described by E. F. Smith under the name *Ps. stewarti* in 1898 from a culture furnished by Stewart. Definite proof by

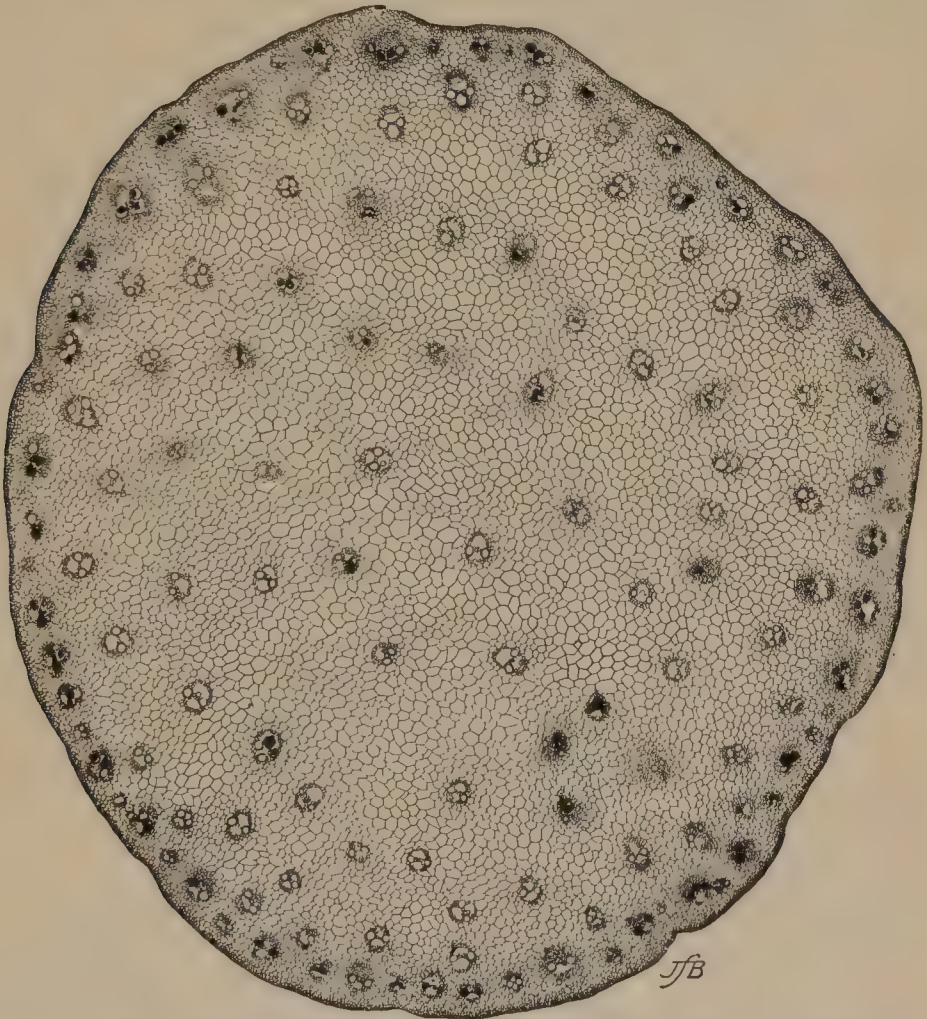


FIG. 15.—Part of sweet-corn stem showing bundles occupied by *Bact. stewarti*. After Smith.

inoculation of the causal relation of this organism to the disease was adduced in 1902 by sprinkling bacteria upon the leaves. Some plants showed typical constitutional symptoms during the first month, most of them in two or three months when the plants were

several feet high. In these plants the vessels became plugged with pure growths of *Bact. stewarti* from tip to base. Small holes filled with yellow slime appeared later in the parenchyma. Infection occurs chiefly through the stomata; wounds are entirely unnecessary. Histological study shows the organisms in the seeds as well as in the ducts of diseased stems. Infection is mainly seed-borne.

Bact. michiganense (E. F. Sm.) Stev.

= *Ps. michiganense* (E. F. Sm.) Stev.

Rod short with rounded ends, $0.35\text{--}0.4 \times 0.8\text{--}1.0 \mu$, viscid, non-motile, aërobic; agar colonies yellow, smooth, round; gelatine slowly liquefied.

The organism was described as the cause of a stem disease of tomatoes in Michigan. Bacteria were present in great numbers in

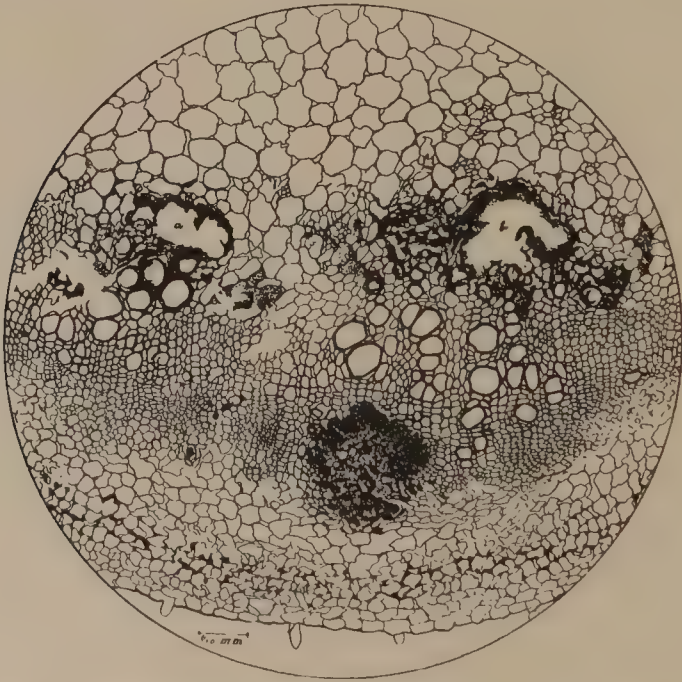


FIG. 16.—*Bact. michiganense* showing effect as seen in cross section of a tomato stem. After Smith.

the bundles; also in cavities in the pith and bark, the seat of the disease being chiefly the phloëm. The organism was isolated and the disease was produced both by pure culture inoculations and by crude inoculations, using an impure inoculum. The disease produced differs from that due to *Ps. solanacearum* in several ways,

particularly in that there is less brown stain in the bundles. It is highly infectious through above-ground parts. The disease spreads by stomatal infection.

Bact. rathayi (E. F. Sm.) Stev.

This organism is of interest because it first appears on the surface of the leaves and only in later stages is it found in the intercellular spaces and in the vascular tissue. The bacterium grows in thick, lemon-yellow, gummy layers enveloping the uppermost leaves and inflorescence. On orchard grass. *Bact. agropyri* is an organism that produces a similar disease on *Agropyron*.

Bact. stizolobii (Wolf) Stev.

Elements cylindrical with rounded ends, single or in pairs, 1–1.6 x 0.6–0.7 μ , non-motile, capsulate, no endospores, zoöglææ not formed; neither acid fast nor stained by Gram's method; colonies on nutrient agar circular, raised, white, shining, margin entire or slightly undulate; gelatine not liquefied; casein partially precipitated and blue color in litmus milk intensified; nitrates not reduced; indol not formed; neither acid nor gas formed in cultures with various sugars; no growth in closed arm of fermentation tubes; no diastatic action; pathogenic on foliage of velvet bean (*Stizolobium*), forming leaf spots which are at first translucent and become at maturity dark brown.

Bact. teutlium Met. is reported as the cause of rot of beets. Several other species have been reported on various hosts abroad, notably on tomato, fig, vanilla, *Wistaria*, orchids, pine, and mulberry.

***Pseudomonas* Migula (p. 14)**

= *Bacterium* Cohn, emend E. F. Sm.

Organism rod shaped, motile by 1–10 polar flagella, most commonly one.

Endospores are sometimes present. The cells in some species adhere to form short chains. The basis of separation into species is the growth upon gelatine, character of the colonies, chromogenesis and numerous other cultural characters.

Numerous species occur as plant pathogens.

Ps. angulata (Fromme and Murray) Stev.¹

A short rod, 0.5 x 2–2.5 μ , no spores, no capsules, motile by 3–6

¹Fromme, F. D. and Wingard, S. A. Black fire or angular leafspot of tobacco. Va. Agr. Exp. Sta. Tech. Bull. 25, 1922.

flagella. Gram negative, aërobic. Agar colony smooth, shiny, opalescent then dull white, gelatine liquefied.

On tobacco leaves causing spots, usually vein-limited, irregularly angular, centers tan, surrounded by a translucent zone, border darker.

Ps. apii Jagger ¹

A short rod, $0.44\text{--}0.87\ \mu \times 0.87\text{--}1.74\ \mu$, one to several polar flagella; colonies on nutrient agar grayish white, shiny, circular, edges entire, flat to slightly raised, granular with age; gelatine liquefied, litmus milk becomes more alkaline, casein peptonized without formation of curd; acid formed from glucose and saccharose, alkali from lactose and glycerine, no gas; no growth in closed arm of fermentation tubes; nitrates not reduced. Parasitic on leaves in celery.

Ps. aptata (Brown and Jamieson) Stev.²

A short motile rod with rounded ends; flagella bipolar; no spores or capsules, aërobic. Agar colonies smooth, whitish; bouillon clouded, gelatine liquefied, fluorescence greenish. T. D. P. $47.5\text{--}48^\circ$. Gram negative.

On nasturtium (*Tropæolum*) and sugar beet leaves causing leaf spots. On nasturtium the spots are brownish and water-soaked, 2–5 mm. in diameter. On beets the spots are irregular, dark brown, often black. The organism was isolated in pure culture from both hosts and from either host produced the disease on both hosts. It is also infectious to bean, lettuce, pepper and egg plant. It appears chiefly to enter through wounds and the bacteria are found in large numbers within the cells. The cell walls become ruptured and collapse.

Ps. atrofaciens (McC.) Stev.

Rods $1\text{--}2.7 \times 0.6\ \mu$, often in long filaments, motile by 1–4 polar flagella, aërobic, no spores, capsulated on beef agar. Peptone-beef agar colonies smooth, shiny white becoming greenish, medium turned green. Gelatine liquefied, milk not coagulated. Gram negative.

On wheat causing lesions at the base of glumes and kernels.

Inoculations are followed by glume discoloration in four days. The discolored tissues abound in bacteria, which penetrate even into the kernels.

¹ Jagger, Ivan C. Bacterial leafspot disease of celery. Jour. Agr. Res. **21**: 185, 1921.

² Brown, Nellie A. and Jamieson, Clara O. A bacterium causing a disease of sugar beet and nasturtium leaves. Jour. Agr. Res. **1**: 189, 1914.

Ps. avenæ Manns. A short rod with round ends, $0.5-1\ \mu \times 1-2\ \mu$. Actively motile, generally by one polar flagellum, occasionally by two or three. Gram negative. What seem to be endospores are found in old cultures. On agar stroke, growth very slow, filiform, rather flat, glistening; margin smooth, opaque to opalescent; non-chromogenic. Liquefaction occurs on gelatine in seven to twelve days. Broth is slowly clouded; agar colonies amorphous, round with surface smooth, edges entire, no gas in dextrose, saccharose, lactose, maltose, or glycerine; ammonia and indol not formed; nitrates reduced to nitrites. T. D. P. 10 min., 60° , Opt. 20° to 30° .

This organism was isolated and described by Manns in 1909, as the cause of a serious oat blight. Inoculations with it alone by hypodermic injection produced only limited lesions but similar inoculations with a mixed culture of *Ps. avenæ* and *Bacillus avenæ* produced typical disease. Manns, moreover, noticed that the virulence of the *Pseudomonas* decreased when kept in culture free from the *Bacillus*, also that in the disease as it occurs in nature these two organisms are associated. His conclusion is that the *Pseudomonas* is the active parasite and that the *Bacillus* is an im-



FIG. 17.—*Ps. avenæ*. After Manns.

portant, perhaps a necessary symbiont. Infection in nature is chiefly stomatal by spattering rain. Soaking of seed in suspensions of bacteria did not produce the disease. Inoculations on wheat failed, though from one variety of blighted wheat, Extra Square Head, the typical organism was isolated. Inoculations on corn made during wet weather produced lesions which spread rapidly and the organism was re-isolated. Barley is said by Manns to be susceptible and what he believes to be the same disease occurs on blue grass and timothy.

Ps. beticola (Sm. Br. & Town.) Stev. causes a disease of beets, in superficial appearance like crown gall.

Ps. campestris (Pam.) E. F. Sm. A rod-shaped, motile, organism generally $0.7-3.0 \times 0.4-0.5\ \mu$; color dull waxy-yellow to canary-yellow, occasionally brighter or more pale. One polar flagellum; no spores known. Aërobic but not a gas or acid producer, gelatine liquefied. Cavities are formed around the bundles but the



FIG. 18.—Showing effect of inoculation of *Ps. campestris* into cabbage plants. Nos. 1 and 2 six weeks after inoculation. No. 3, check plant uninoculated. After Russell.

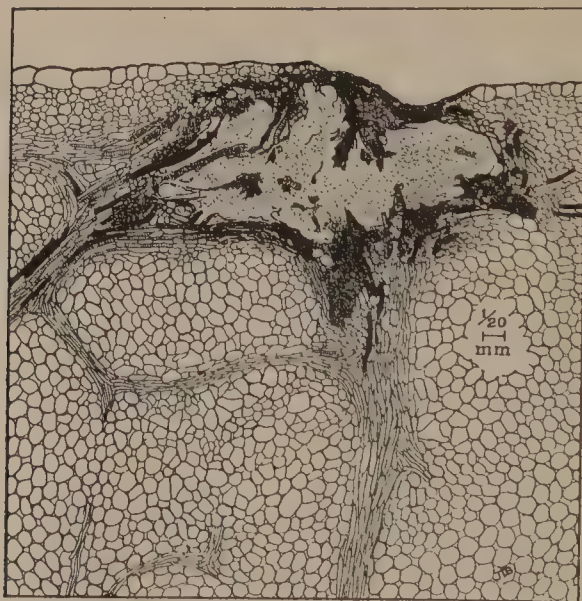


FIG. 19.—*Ps. campestris*. Section of a cabbage leaf parallel to the surface and near the margin, showing the result of infection through the water pores. After Smith.

organism seems to be only feebly destructive to cellulose. A brown pigment is produced in the host plants and on steamed cruciferous substrata. Growth rapid on steamed potato cylinders at room temperatures, without odor or brown pigment. Growth feeble at 7°, rapid at 17 to 19°, luxuriant at 21 to 26°, very feeble at 37 to 38°, and ceases at 40°. T. D. P., 10 min., 51°.

It is troublesome upon cabbage, turnips, cauliflowers, collards and a very large number of cruciferous hosts, both cultivated and wild, are susceptible.

The chief seat of infection is the ducts which become filled with the bacteria and are blackened.

This organism was first isolated by Pammel from rutabagas and yellow turnips in 1892; green-house inoculations with pure cultures were made in scalpel wounds, which were then sealed with wax. The plants showed rot in a few days and the actual causal relation of the

organism was thus established. It was later shown that the cabbage and turnip organisms are identical and that the bacteria, by solution of the cellulose, produce pits and holes through the walls of the host cells resulting eventually in large cavities.

Dissolution of tissue is accomplished chiefly by occupation of the

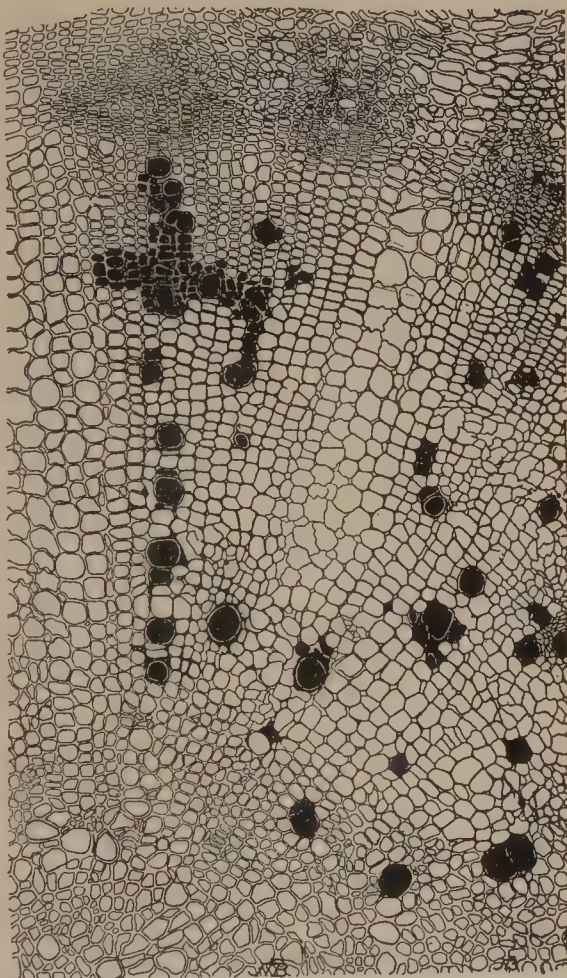


FIG. 20.—Cross-section of turnip root showing vessels filled with *Ps. campestris*. After Smith.

intercellular spaces followed by solution of the middle lamellæ and finally by squeezing the elements apart.

Infection is chiefly through the water pores or through wounds made by insects; the bacteria being air or insect borne and derived largely from infected soil. After entering the plant the bacteria multiply rapidly, and migrate in every direction by means of the veins.

The organism can survive the winter on the seed and thus infect seedlings.

Ps. cannæ (Bryan) Stev.¹

A short rod with rounded ends; flagella 1-3, bi-polar; capsules present; no pseudozoöglææ, aërobic, non-chromogenic, liquefies gelatine very slowly, does not produce acid or gas from sugars; clears milk; blues, then reduces litmus milk without coagulation, does not produce indol. Optimum temperature 35° C., maximum 40°, minimum 5°; T. D. P. 52°. Gram negative.

The cause of meristematic disease in cultivated cannas.

Ps. cerasi Griffin²

Short rods 1.5-2.5 x 0.5-0.8 μ , motile by 1 or 2 polar flagella, no spores. Gram negative. On agar, flat, glistening, greening the medium; gelatine liquefied.

The cause of blight of buds and fruit spurs of cherry accompanied by gummosis; also of girdling of limb or trunk.

Ps. citrerefaciens (Lee) Stev.³ A rod with 1-4 polar flagella. It causes "Citrus Blast" in which the young leaves drop off.

Ps. citri Hasse

A short motile rod with rounded ends and one polar flagellum, 1.5-2 x 0.5-0.7 μ . Agar colonies circular, entire, smooth, dull yellow. On potato a bright yellow streak, slimy. Casein precipitated, gelatine liquefied.

On citrus causing canker also fruit and leaf spots. Infection is produced with or without wounds by means of pure cultures. The host cells are stimulated to abnormal growth and the tension ruptures the epidermis. Diseased cells are filled with the bacteria. The distinction between palisade and parenchyma is obliterated and all the cells are somewhat enlarged and distorted. In later

¹ Bryan, Mary K. A bacterial budrot of cannas. Jour. Agr. Res. **21**: 143, 1921.

² Barss, H. B. Cherry gummosis. Ore. Agr. Exp. Sta. Crop Pest and Hort. Rept. 199, 1911-1912.

³ Lee, H. Atherton. A new bacterial citrus disease. Jour. Agr. Res. **9**: 1, 1917.

stages some of the cells disintegrate. Bacterial action is more pronounced on the cell contents than on the walls.

Ps. citriputealis (C. O. Sm.) Stev.¹

Actively motile rods with a single polar flagellum, $2-4 \times 0.5-1 \mu$, aerobic, no capsule or spores. Agar colonies pearl gray, 2-5 mm., gelatine slowly liquefied. Circular, black, depressed, dry-rot spots, 5-20 mm. in diameter, are produced in the rind of lemons; inoculations were made with pure cultures by pricking and by atomizing, spots resulting in three or four days.

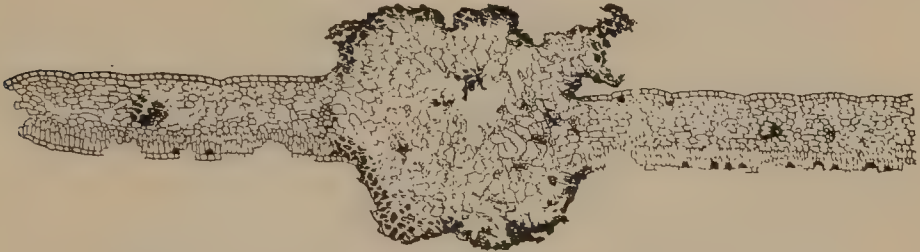


FIG. 21.—Section of a portion of a grapefruit leaf bearing a young canker caused by *Ps. citri*. After Hasse.

Ps. coronafaciens (Elliott) Stev.²

Rod, $2.3 \times 0.65 \mu$, motile by polar flagella, no spores, capsulate; agar colonies white, gelatine liquefied slowly, casein digested without curdling. Gram negative.

Pathogenic in oats and to less extent on wheat, rye, and barley. Spots ovate, chlorotic, 0.5-2 cm. or larger. Centers of gray-brown, collapsed tissue surrounded by a halo, at first light green, later yellow. Bacteria present in the centers, probably absent from the halo, at first intercellular but later they destroy the cell walls and cause collapse.

Ps. flaccumfaciens (Hedges) Stev. causes disease of beans.

Ps. dissolvens Rosen

Short rods, motile by means of a single polar flagellum, capsules present, no spores, white on most solid media; colonies round, margins entire, white, opaque, glistening, emitting a strong odor of decaying vegetable matter; gelatine not liquefied; acid and gas produced on most nutrient media. It is the cause of rot of the roots of corn and of adjacent stem with purplish discoloration.

¹ Smith, C. O. Black pit of lemon. *Phytop.* **3**: 277, 1913.

² Elliott, C. Halo blight of oats. *Jour. Agr. Res.* **19**: 139, 1920.

Ps. vesicatoria (Doidge) Stev.¹=Bact. exitiosum Gardner & Kendrick.

Cylindrical rods, rounded at the ends, solitary or in pairs; individual rods 1.5–2.7 x 0.6–1.3 μ ; motile by a single polar flagellum; aerobic, no spores; superficial colonies on potato agar, round, pulvinate, smooth, glistening, naphthalene yellow, with radial striae of color in peripheral zone; margin entire. Gelatine rapidly liquefied; no acid produced in milk; digests casein; Gram negative. The cause of a spot disease in fruit, stem and leaves of tomato.

Ps. erodii Lewis is described as pathogenic on *Erodium* and a large number of varieties of cultivated "geraniums."

Ps. fluorescens (Flügge) Mig. or varieties of it are held responsible for a decay of celery, and of producing wet rot of various vegetables, carrots, rutabagas, tobacco, tomatoes, melons.

A disease of mushrooms is also caused by this or a very closely related organism.

Ps. glycinea Coerper

Rods 2.3–3 x 1.2–1.5 μ , motile by 1–several polar flagella; no spores; capsulated on blood agar. Potato agar colonies round, shiny, with umbonate center, creamy to brownish. No gelatine liquefaction, casein not digested, Gram negative. T. D. P. 48–49°.

Forming small angular lesions on soy bean. Young spots are translucent, old are dark reddish-brown to black. Spots 1–2 mm. in diameter, often confluent. Infection is stomatal, the bacteria invading the parenchyma intercellularly. Inoculation by atomizing unwounded leaves gives spots in about 10 days.

A closely related organism was described by Wolf under the name Bact. *sojæ* as the cause of a similar disease of soy beans.

Ps. juglandis Pierce. A rod 1–2 x 0.5 μ , with rounded ends, actively motile by one long polar flagellum. Bright chrome-yellow in growth; disastatic ferment present. No gas; aerobic. It was isolated from diseased nuts, leaves, and twigs of English walnut in California in 1901. Inoculations by spraying demonstrated its pathogenicity. The organism is closely related to *Ps. campestris* but is distinguished from it by the abundant, bright yellow pigment produced upon the surface of extracts of leaves of walnut, magnolia, fig, castor bean and loquat.

In young walnuts the epicarp, forming shell and kernel, are destroyed. Leaves are attacked along the veins and on the pet-

¹Gardner, Max W. & Kendrick, James B. Bacterial spot of tomato. Jour. Agr. Res. **21**: 123, 1921.

ioles, the bacteria often entering the vessels. All tissues in branches are destroyed, the bacteria entering and wintering in the pith. Infection is stomatal.

Ps. lachrymans. (Sm. & Bryan) Carsner. Rod $0.8 \times 1-2 \mu$, with rounded ends, motile by 1-5 polar flagella, aërobic, non-sporing. Gelatine slowly liquefied. Agar surface colonies circular, white, no gas. Gram negative. On cucumber leaves forming angular, water soaked, exudating spots. Infection of the leaves and fruit is through the stomata and occurs more readily when the stomata are open. Small spots result in about five days. In these the bacteria occupy the intercellular spaces, and crowd apart and crush the parenchyma, causing swelling and exudation. In age the diseased area becomes dry, brown and dead.

Ps. maculicola (McC.) Stev. A short rod, forming long chains in some media. Ends rounded. Size from leaf $1.5-2.4 \mu \times 0.8-0.9 \mu$; in 24-hour beef-agar culture, $1.5-3 \mu \times 0.9 \mu$. No spores, actively motile, one to five polar flagella, two to three times the length of the rod. Motile in most artificial media. Involution forms in alkaline beef bouillon. Pseudo-zoöglææ in Uschinsky's solution. Gram negative. Stains readily with carbol-fuchsin and with an alcoholic solution of gentian violet.

Agar plate colonies visible on the second day as tiny white specks, in three to four days, 1-3 mm. in diameter, white, round, smooth, flat, shining, and translucent, edges entire, with age dull to dirty white, slightly irregular, edges undulate, slightly crinkled, and with indistinct radiating marginal lines. Buried colonies small, lens-shaped.

Agar streak cultures white, margins slightly undulate. Beef bouillon clouds in twenty-four hours. Growth best at surface where a white layer, not a true pellicle, is formed. No zoöglææ; no rim.

Gelatine stab cultures liquefied in eight to ten days. Growth from surface crateriform; slight, white, granular precipitate. Slight green fluorescence. No separation into curd and whey. Indol production feeble. T. D. P. 46° . Opt. $24-25^{\circ}$. Max. 29° . Min. below 0° .

Isolated from cauliflower leaves on which it forms brownish to purplish-gray spots 1-3 mm. in diameter. Pathogenicity on this host also on cabbage was proved by atomizing. Its entrance is stomatal, and specks 1-3 mm. in diameter in the green leaves, result, both on the veins and in the parenchyma.

Ps. malvacearum E. F. Sm. This yellow organism, pathogenic on cotton, much resembles *Ps. campestris* but its slime is more translucent on potato and it does not attack the cabbage. It is Gram negative, non-acid-fast, non-sporing, motile and polar flagellate. It was grown in pure culture and successful inocula-

tions were made by atomizing a suspension of a young agar culture of the organism upon cotton leaves and bolls. Infection is largely stomatal, the intercellular, substomatal spaces becoming filled with bacteria. Minute water-soaked spots result in from 12-20 days.

Ps. marginalis (Brown) Stev. A short rod, motile by 1-3 bipolar flagella, capsulate, no spores, aërobic. Agar colonies cream colored, later yellow. Agar colored green. On potato dirty-cream colored, later buff. Gelatine liquefied, fluorescence green. T. D. P. 52-53.°

On lettuce causing marginal brown to black dead spots which become dry and papery.

Ps. medicaginis Sackett. A short rod, 1.2-2.4 x 0.5-0.8 μ ; filaments 20.2-37.2 μ long. No spores; actively motile with 1-4 bipolar flagella; capsules and zoöglæe none. Agar

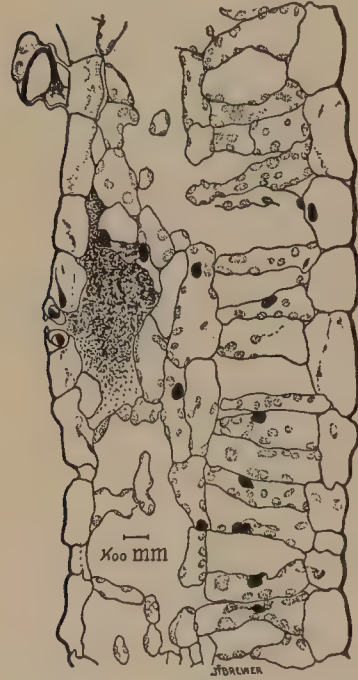


FIG. 22.—*Ps. malvacearum*. Early stage of stomatal infection in angular leaf spot of cotton. After Smith.

streak filiform later echinulate, glistening, smooth, translucent, grayish-white; no gelatine liquefaction; bouillon slightly turbid, pellicle on third day, sediment scant. Milk unchanged. Agar colonies round, grayish-white. No gas or indol. Optimum reaction + 15 to + 18. Fuller's scale. T. D. P. 49-50°, 10 min. Opt. 28-30°. Aërobic. No diastase, invertase, zymase, rennet or pepsin.

It occurs as a pathogen on alfalfa and issues in clouds visible to the naked eye from small pieces of tissue of the diseased stem or leaf when mounted in water on the slide. These clouds under the high power resolve into actively motile rods, relatively short and thick. The bacteria are also found in practically pure culture in

the exudate which oozes from the diseased tissues as a clear viscous liquid and collects in drops or spreads over the stem. In early stages the stem is watery, semi-translucent. In late stages disease extends to the center of the stem and the interior is brown. Disease also occurs on petioles and leaves. Sackett with pure culture inoculations produced the typical disease and re-isolated the organism with unchanged characters. Re-inoculated, it again caused disease. Infection, stomatal or water pore, was also secured through the apparently unbroken epidermis. It is believed that the usual mode of infection is through rifts in the epidermis due to frost and that the germ is wind-borne from infected soil.

Ps. mellea Johnson. A short rod with rounded ends. Average size $0.6 \times 1.8 \mu$. Motile by a tuft of polar flagella usually two to three in number, three to five times as long as the body of the organism. No

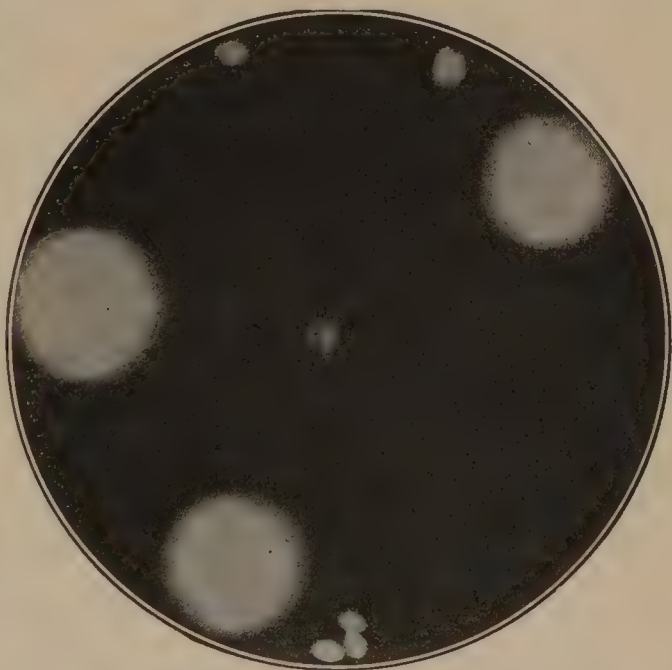


FIG. 23.—*Ps. medicaginis*; agar colonies 7 days old, deep and surface colonies by reflected light. After Sackett.

spores or involution forms observed. Capsules present. It is Gram-negative and not acid-fast, pale or orange yellow on most media. In gelatine stabs growth is best at top with liquefaction beginning in 3 days and complete in about 20 days. Coagulation of milk is prompt.

Parasitic on tobacco causing leaf spots. The leaf spot of tobacco differs from both the wildfire leaf spot and the angular leaf spot and manifests itself by round, brown, or rust-colored spots, usually less than a half inch in diameter, but frequently running together to form larger irregular lesions. Frequently the young

lesions are marked by a distinct chlorotic area or halo surrounding the point of infection.

Ps. mori (B. & L.) Stev. Rod with rounded ends, 1.8–4.5 x 0.9–1.3 μ , mostly 3.6 x 1.–2 μ ; motile by 1–7 polar flagella. No spores. Pseudozoöglææ present. Agar colonies round, smooth, flat. Agar streaks spreading, flat, dull-white. Gelatine stab filiform, no liquefaction. Milk not coagulated. No gas. T. D. P. 51.5°.

This organism causes a blight of mulberries much resembling pear blight. The bacteria invade both wood and bark though disease is principally of the bark. On the leaves water-soaked spots form and eventually turn dark. Bacteria are in the intercellular spaces and produce cavities.

In 1894 Boyer and Lambert produced successful inoculations on mulberries with an organism to which they gave the above name, but without description.

In 1908 E. F. Smith plated out, from blighted mulberry leaves collected in Georgia, a white species with which he made numerous infections on both stems and leaves of mulberry. From these cultures Smith supplied the description quoted in part above.

Ps. papulans Rose causes rough-bark or scurfy bark of apples.

Ps. pelargoni (Brown) Stev. A motile rod with one polar flagellum causes a bacterial leaf spot disease of the cultivated geranium.

Ps. phaseoli E. F. Sm. A short, round-ended rod, wax-yellow to chrome-yellow, motile, polar-flagellate, anaërobic. Milk coagulates, and the whey slowly separates without acidity; gelatine liquefies slowly. Growth feeble at 37°, none at 40°. T. D. P. 10 min., 49.5°. A starch enzyme is produced and the middle lamella also dissolved.



FIG. 24.—*Ps. phaseoli*.
After Smith.

This organism is pathogenic to beans and some related legumes and is closely related to *Ps. campestris*; a variety of it has been described on soy bean. The disease on leaves, stems and pods is principally of the parenchyma though

ducts are occasionally invaded to a distance of several centimeters. On leaves a few days after infection minute translucent dots appear; these enlarge and, due to collapse of the tissues, become sunken. On pods the fleshy pericarp is rotted; the bacteria infect the developing seed and surface bacterial ooze is present. Infection is largely stomatal.

Ps. pisi Sackett. A short rod, $1.11\text{--}3.28 \times 3.28 \times 0.58\text{--}0.82 \mu$, no spores, no capsule, no zoöglææ, motile by one polar flagellum. Gram negative, Agar stroke filiform, grayish-white. Gelatine liquefied. Milk coagulated, later peptonized.

On garden peas. The affected stems are watery olive green to olive brown, attacked petioles soon assume the same color and collapse. Infection is by way of stomata or wounds. The substomatal chambers are crowded with bacteria, also many of the adjacent cells. Inoculation and reisolation establish the pathogenicity of the organism.

Ps. pruni E. F. Sm. The organism resembles *Ps. campestris* but is distinguished from it by its feebler growth on potato and

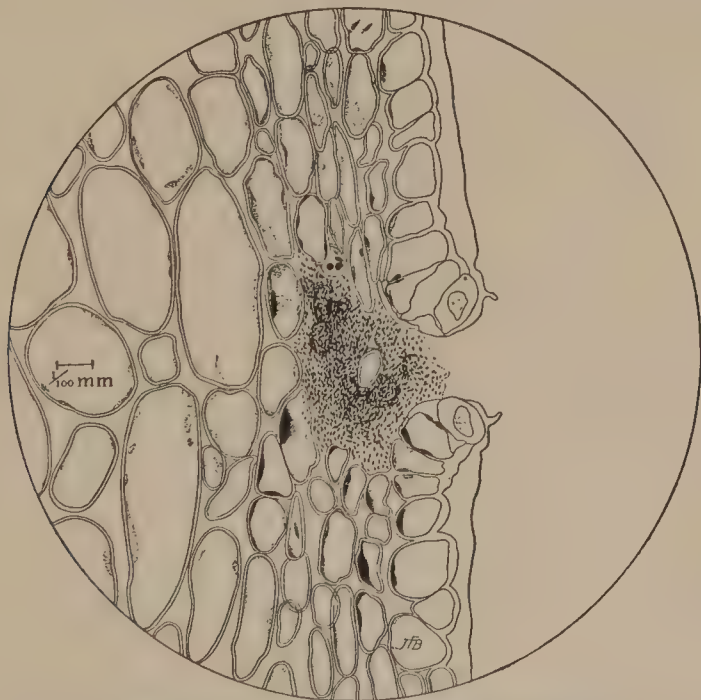


FIG. 25.—Earliest stage of fruit spot on green plums, due to *Ps. pruni*. The bacteria entered through the stoma. After Smith.

by its behavior in Ushnisky's solution which it converts into a viscid fluid. It consists of small rods, motile by one to several polar flagella. T. D. P. 51° .

On apricot, nectarine, peach and plum, causing leaf, twig and fruit disease.

The bacteria enter through the stomata or lenticels and cause

watery spots on green fruit and leaves, and finally the death of the affected tissue. Cankers are also produced on the twigs. In earliest disease the infection is limited to the substomatal space, but gradually invades more distant tissue. Parenchyma is chiefly affected, but phloëm and xylem are also attacked. By numerous cultures and cross inoculations it was proved that this organism is responsible for the disease.

Ps. rhizoctonia (Thomas) Stev.

A rod shaped organism, not motile, colony circular, olive buff in color when incubated in the dark, pyrite yellow in subdued light. Does not stain by Gram's method, not acid-fast. Gives good reduction of nitrates within 24 hours. Characteristic color constant on all ordinary media such as potato agar, plain nutrient agar, potato plugs, rice, oatmeal agar.

It causes retarded development or a rosette disease of lettuce accompanied by a yellowing or flaccid condition of the outer leaves.

The small fibrous roots are apparently attacked first at their tips. The infection slowly progresses upward until the larger roots are invaded. No rot or spots upon the leaves or stems. The chief rôle of the organism seems to be to attack the root hairs and small fibrous roots of the lettuce plant, gain entrance into the vascular system and interfere with the free passage of materials.

Ps. savastanoi (E. F. Sm.) Stev. A rod with rounded ends, solitary or in short chains, $1.2-3 \times 0.4-0.8 \mu$; motile, aërobic, non-sporeing, flagella 1-4, polar. Standard agar surface colonies, white, small, circular, smooth, 1.5-3 mm. at three days, edge entire; bouillon thinly clouded, precipitate slight, white. On gelatine no liquefaction; colonies white, round, erose, margin pale.

From tubercles on Californian olive branches, the causal organism, which is in part *Ps. oleæ-tuberculosis* Sav. and which may bear relation to several other olive bacteria previously described in Europe, was isolated.

The organism when inoculated by puncture into young olive shoots produced the characteristic tubercle. Later it was re-isolated from these artificially produced tubercles and used in a second series of inoculations which gave a second crop of tubercles. The oleander was not susceptible to infection though a similar tumor occurs on this host. A like disease is also on ash but the causal organism is slightly different.

This organism causes marked hypertrophy on roots, trunk,

branches and leaves of olives, resulting in tumors, large or small, spongy or cheesy, which soon decay. The disease is perennial and spreads yearly into both new and old wood. Secondary tumors occur near or distant from old ones, but without connecting strands. The bacteria are abundant between the host cells and later in the intercellular spaces where they develop irregularly branched cavities. Infection may occur from the surface through wounds or from the interior by migration of bacteria through the ducts. Such ducts are browned and somewhat disorganized. The tumor may consist of both wood and cortex, the vessels being reduced and the parenchyma greatly increased.

Ps. solanacearum (E. F. Sm.) Stev.¹=*Bacillus solanacearum* E. F. Sm.=*Bact. solanacearum* (E. F. Sm.) E. F. Sm. A medium sized, easily stained, strictly aërobic bacillus with rounded ends; about $1\frac{1}{4}$ -3 times longer than broad; $0.5 \times 1.5 \mu$. Motile, sluggish or active; flagella polar. Spores not known. Zoöglææ occur in liquid media as small, white flecks or as surface rings. It grows well at 20-30°. Milk is saponified with no casein precipitation or acidity; gelatine not liquefied; agar surface colonies dirty-white; agar streaks first dirty-white, later yellowish to brownish-white, then brown; on potato as on agar, but darker, with substratum and fluid browned; no gas from cane sugar, lactose, maltose or dextrose.

The disease caused by this bacillus upon tomato and other plants was early studied by Halsted who made inoculations which produced the disease, but he did not use pure cultures.

In its hosts the bacillus is found in the pith, in the xylem which is browned, and more rarely in the bark. It is, however, primarily a vascular disease and from the cut ends of infected ducts bacteria exude as a viscid ooze. The diseased ducts are browned and may be traced to great distances through the plant, even from root to leaf. From the bundles the organism later invades other tissues, often with great destruction of pith and bark, honey-combing the pith with cavities. Infection is commonly through wounds, often by way of broken roots, but is sometimes through stomata.

Needle prick inoculations in tomatoes by Smith, with pure cultures, were followed after several weeks by typical disease. Inoculations in Irish potato resulted similarly, though in this host the parenchyma and bark were eventually invaded, and the tuber

¹ Smith, E. F. Bacterial diseases of plants.

was reached through its stem end and rotted. In South Carolina, Smith noted the disease on egg plants and crude cross inoculations were made in tomato. He demonstrated experimentally the efficiency of the potato beetle in transmitting the disease.

The disease was described for tobacco by Stevens and Sackett. Successful inoculations were reported upon tobacco by E. F. Smith in 1909. In addition to the above hosts it is known to grow upon

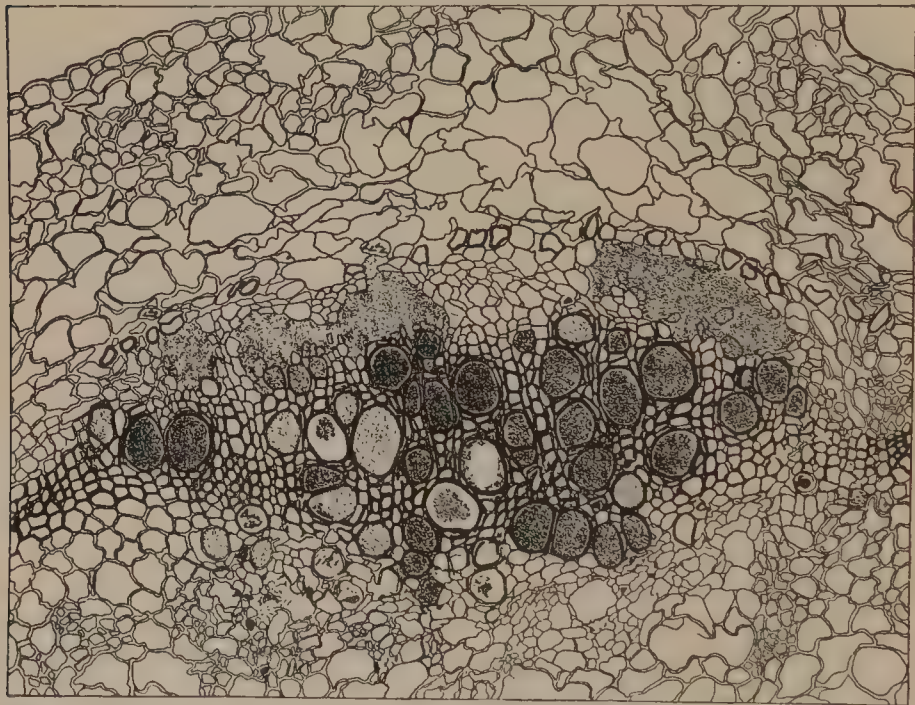


FIG. 26.—*Ps. solanacearum*: cross-section of a potato stem showing bacteria in the ducts.
After E. F. Smith.

Datura, *Solanum nigrum*, *Physalis* and *Petunia*, nasturtium, peanut, bean, pea, *Ricinus*, vanilla, *Helianthus*, *Dahlia* and *Cosmos*.

B. nicotianæ Uyeda, said to cause a wilt of tobacco in Japan closely resembling that caused by *Ps. solanacearum*, may be this same organism.

Ps. tabaci (Wolf and Foster) Stev.

Rod motile by 1 polar flagellum, $2.4-5 \times 0.9-1.5 \mu$, Gram negative. Potato agar colonies gray-white, circular. Gelatine liquefaction slow. T. D. P. 65° .

On tobacco leaves producing water-soaked spots, at first chlorotic, 0.5–1. cm. in diameter. Brown, dead areas soon develop

in the centers. Bacteria abound in the intercellular spaces and in old lesions within the cells.

***Ps. translucens* J. J. & R.**

Rods 0.5–0.8 x 1–2.5 μ , motile by one polar flagellum, aërobic, no spores. Agar colonies entire, smooth, shiny, wax-yellow. Gelatine slowly liquefied, casein digested. Gram negative.

On barley leaves causing translucent spots.

The leaf spots are watery, extend longitudinally, and are largely vein-limited. Infected tissues later become yellow, then brown. Bacterial exudation occurs under humid conditions and the exudate dries to resinous granules. Infection is stomatal and the bacterial invasion is in the parenchyma, largely through the intercellular spaces; the cell walls disintegrate.

Ps. translucens* var. *undulosa causes black chaff of wheat in which black sunken stripes, swarming with bacteria, occur on the glume. In late stages the rachis and stalk are also striped.

***Ps. tumefaciens* (S. & T.) Stev.** Vegetative cells taken directly from a gall usually 0.6–1.0 μ x 1.2–1.5 μ . Endospores not observed; motile by means of one, sometimes two or three terminal flagella; viscid on agar; readily stained in ordinary basic anilin stains. Gram. negative; agar surface colonies, white, smooth, circular; margin even, shining, semi-transparent, maximum size 2 to 4 mm.; agar streak growth moderate, filiform; on sterile potato cylinders growth more rapid, in one or two days covering the entire surface of the cylinder; smooth, wet-glistening, slimy to viscid, odorless; potato cylinder grayish, darker with age, never yellow; gelatine colonies dense, white, circular; small, non-liquefying, medium not stained; in beef broth clouding often absent or inconspicuous, rim of gelatinous threads present, also more or less of pellicle; milk coagulation delayed; litmus milk gradually blued, then reduced; no gas produced; organism aërobic in its tendencies; nitrates not reduced; indol produced in small quantity, slowly. T; D. P. 51°. Opt. between 25° and 28°, Max. 37°. Growth occurs at 0°. Milk, bouillon, dextrose peptone water with calcium carbonate are the best media for long continued growth.

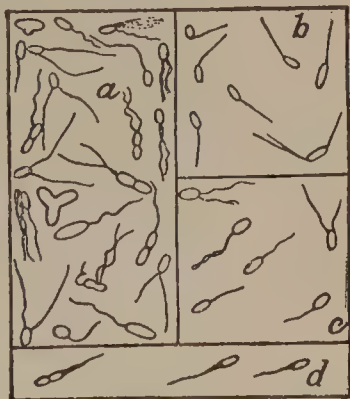


FIG. 27—Flagella of *Ps. tumefaciens*. After Smith.

The cause of crown gall on a wide range of hosts.

In galls on the Paris daisy these bacteria were found in small numbers. By plating they were obtained in pure culture and puncture inoculations repeatedly resulted in the characteristic gall.

From these the organism was re-isolated and the disease again produced, thus giving conclusive evidence that the organism is the actual cause of the gall. Swellings began four or five days after inoculation and in a month they were well developed, though they continued to enlarge for several months, reaching a size of 2-5 cm. in diameter.

The disease produced is peculiar in that the cells attacked are not killed but are stimulated to multiply, the result being a largely hyperplastic parenchyma, poorly supplied with vessels, forming either a hard or a soft tumor which varies in size up to more than four feet in diameter. Secondary tumors develop at various, often considerable, distances from the primary tumors and are connected with them by a continuous chain of diseased cells, the tumor strand. The secondary tumors have the tissue



FIG. 28.—Cross-section of stem between primary and secondary tumors, showing large-celled tumor-strand with big nuclei. After E. F. Smith.

structure of the region in which the primary tumor is located, e. g., if the primary tumor is in a stem and the secondary tumor in a leaf the secondary tumor will have the structure characteristic of stems. The causal organism occurs in small numbers inside of the host cells and as the cells divide bacteria go to each daughter cell. They are difficult to see when in tissues and require special stains.

Tumor-producing Schizomycetes have been isolated from over-

growths on plants belonging to many widely separated families (Compositæ to Salicacæ) and galls have been produced by inoculation, using the daisy and hop organism, on some 40 kinds of plants belonging to 18 families. Natural galls have been studied on *Chrysanthemum*, peach, apple, rose, quince, honeysuckle, *Arbutus*, cotton, poplar, chestnut, alfalfa, grape, hop, beet, salsify, turnip, parsnip, lettuce, and willow. The organisms from these sources are closely alike on various culture media, and many of them are readily cross-inoculable, e. g., **daisy** to peach, radish, grape, sugar-beet, hop; **peach** to daisy, apple, *Pelargonium*, sugar-beet, poplar; **hop** to daisy, tomato, sugar-beet; **grape** to almond, sugar-beet; **poplar** to cactus, oleander, sugar-beet; **willow** to daisy. In general it is said that all plants susceptible to crown galls, i. e., those on which the galls have been found in nature, are susceptible to artificial cross inoculation. Hard gall, hairy root, and soft gall are also all due to infectious bacteria.

Smith states that the hairy root organism and the crown gall organism are identical and that if infection takes place in certain tissues an ordinary gall will develop, while if other tissues are first invaded, then a cluster of fleshy roots will develop.

Ps. vignæ Gardner & Kendrick causes a rather destructive bacterial disease of cowpeas characterized by spots on the leaves, stems and pods.

Ps. viridilivida (Brown) Stev.

Rod motile, by 1-3 polar flagella, gelatine liquefied slowly. On potato cylinders a fleeting dark blue-green color. Gram positive. Agar colonies round, entire, smooth, cream-white.

On lettuce leaves producing spotting. The bacteria are both in the cells and between them.

Ps. vitians (Brown) Stev.

A short rod motile by bipolar flagella, capsulate, no spores, aërobic. Agar colonies, light-cream color, smooth, thin, round. On potato yellow. Gelatine liquefied. Gram negative. T. D. P. 51-52°.

On lettuce leaves producing spots and rot and in stems producing rot.

Ps. woodsii (E. F. Sm.) Stev. causes spots on carnation leaves, infection occurring through the stomata.

Other species have been reported on iris, gladiolus, hyacinth, syringa, sugar-cane, Lima bean, clover.¹

¹ Jones, L. R., Williamson, M. M., Wolf, F. A., McCulloch, Lucia. Bacterial leafspot of clovers. Jour. Agr. Res. **25**; 471, 1923.

Bacillus Cohn (p. 14)

This genus differs from *Pseudomonas* only in its peritrichiate, not polar, flagella. Endospores are often present. Of the four hundred and fifty or more species fourteen are given here as plant pathogens. Numerous animal pathogens also belong to this genus, notably *B. typhosus*, *B. pestis*.

***B. amylovorus* (Burr.) Trev. = *Erwinia amylovora* (Burr.) Committee.**

Bacillus in broth, $0.9-1.5 \times 0.7-1.0 \mu$, longer when older. Gram negative; no capsule; flagella several, peritrichiate; no spores; broth clouded, pellicle slight. Gelatine shows slow, crateriform liquefaction; agar buried colonies white, surface colonies elevated, circular, wet-shining, margin irregular; milk coagulated in three-fourths of a day, later digested to a pasty condition. Opt. $25-30^{\circ}$. T. D. P. 43.7° , 10 min. Facultative anaërobe. Indol produced; no gas; no pigment.

Bacteria were noted in blighted pear twigs by Burrill in 1877. In 1880 he demonstrated the communicability of the disease by introducing the bacterial exudate into healthy pear trees as well as into apple and quince trees. This constitutes the first case of plant disease definitely attributed to bacteria. Burrill's results were confirmed by Arthur in 1884 by one hundred and twenty-one puncture inoculations, using the exudate, also a bacterial suspension from diseased twigs. He further demonstrated the susceptibility of Juneberry and hawthorn.

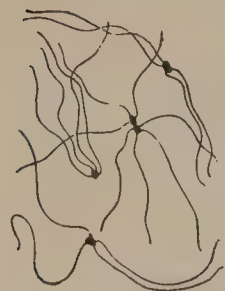


FIG. 29.—*B. amylovorus*, multiplying by fission. After Whetzel and Stewart.

Arthur placed the whole matter on a firm foundation by passing the bacteria through a long series of artificial cultures and then by inoculations, showing that they were capable of causing the blight. He further demonstrated that the bacterial exudate from the tree, when freed of bacteria by filtration, could not produce disease. The results of an extensive study of the bacteria on various media, of their morphology and stain reactions, were published by Arthur in 1886. Bacteria were shown to penetrate twigs 3-4 dm. beyond their area of visible effect.

In 1902 Jones isolated an organism from blighted plum trees. This he demonstrated by culture and cross inoculation in fruits to be identical with the pear blight organism, though inoculations in

plum twigs did not give disease, presumably due to the high resistance of this plant. Similarly Paddock has shown this organism to attack the apricot.

Other hosts are hawthorn, shad bush, mountain ash, loquat, strawberry and cherry, and possibly the blackberry.

By inoculations with pure cultures of the apple body-blight bacteria, blight upon twigs and blossoms was produced by Whetzel in 1906 thus proving the identity of these two forms of disease, an identity asserted first by Burrill.

The bacteria enter the host either through wounds or through the nectaries. The first evidence of infection is a transparency of the diseased tissue, probably due to removal of air from the intercellular spaces, later followed by browning. The bacteria abound in the spaces between cells also in the ducts, and in late stages of disease the host cells are plasmolyzed. In the shoots disease is chiefly of the bark and it advances through the bark parenchyma. The organism disintegrates fruits by multiplying in the intercellular spaces and dissolving the middle lamellæ.

B. atrosepticus van Hall.^{1, 2}

Short rods, long rods, short chains, long chains, 0.4–0.8 x 1–2 μ or more. Endospores none; flagella few, not over 6 or 8. Attachment peritrichiate; capsules none. Agar stroke filiform, flat to slightly raised, luster glistening, surface smooth, slightly but distinctly bluish opalescent, pearly-white. Gelatine liquefaction, infundibuliform to slightly napiform, or saccate.

This organism is said by Morse to cause potato black-leg and to be identical with *B. solanisaprus* Harr. and to be distinct from *B. phytophthorus* Appel. See p. 45.

B. avenæ Manns. This is the symbiont of *Pseudomonas avenæ*. See p. 30.

A very actively motile bacillus, short, rod-shaped with rounded ends, 0.75–1 x 1.5–2 μ . Gram negative; endospores not observed; flagella many, diffuse, long, undulate; growth on agar stroke rapid, filiform, white, glistening, later somewhat dull, margin smooth, growth rather opaque, turning yellow third day; gelatine not liquefied; broth clouded and on the second day showing heavy yellow precipitate; milk coagulated at end of two weeks

¹ Morse, W. J., Studies upon the black-leg disease of the potato, with special reference to the causal organisms. Jour. Agr. Res. 8: 122, 1917.

² Paine, Sydney G. and Chaudhuri, H., The black-leg disease of the potato. On the relationship of *Bacillus atrosepticus* and *Bacillus solanisaprus*. Phytop. 13: 359, 1923.

with extrusion of whey; agar colonies round, entire, surface smooth, slightly raised. No gas in dextrose, saccharose, lactose, maltose, or glycerines. Indol production moderate; nitrates reduced to nitrites. T. D. P. 10 min., 60°; Opt. 20–30°.

B. carotovorus L. R. Jones = *Erwina carotovora* (Jones) Committee. From agar 1–2 days old as short or long rods, in short or long chains. $0.6\text{--}0.9 \times 1.5\text{--}5 \mu$, commonly $0.8 \times 2 \mu$; ends rounded. No spore; flagella 2–5, peritrichiate; no capsule. Gram negative;

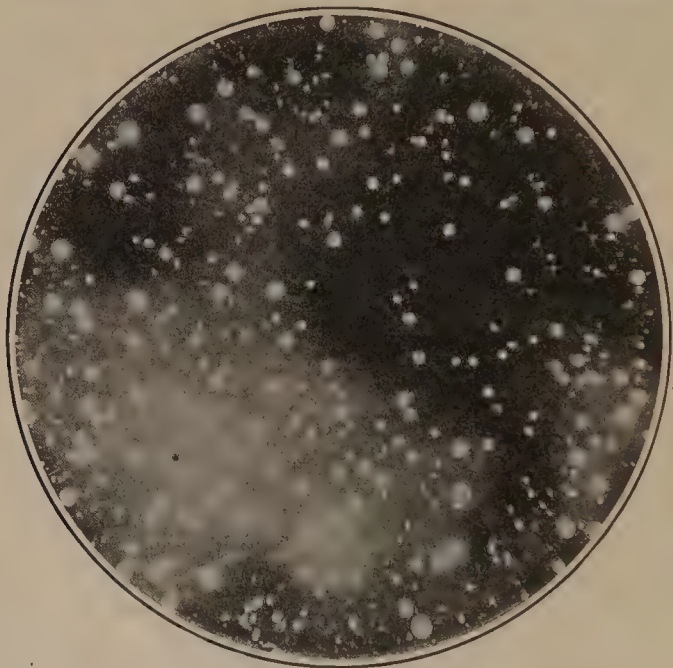


FIG. 30.—Plate culture of *B. avenae*, on nutrient glucose agar four days at 30° C. After Manns.

white on all media; agar slope filiform to spreading, glistening, opaque to opalescent. Gelatine liquefaction crateriform to infundibuliform. Broth clouded, pellicle thin to absent, sediment flocculent; milk coagulated. Agar colonies, round, smooth, entire to undulate, amorphous or granular. Some gas in dextrose, lactose and saccharose, nitrates reduced to nitrites; indol feeble. T. D. P. 51°. Opt. 25–30°.

A considerable number of cultivated plants undergo soft rot of the parenchyma from the attacks of a non-chromogenic liquefying bacillus. Among the plants so affected are cabbage, turnips and other crucifers; parsnip, carrot, mangel, sugar-beet, potato, cel-

ery, tomato, Jerusalem artichoke, asparagus, rhubarb, onion, iris, calla and Colocasia.

In 1901, Jones reported an organism isolated from rotting carrots which he named *B. carotovorus*. It disorganized tissue by solution of the middle lamellæ, and infection into wounds led to decay of the roots of carrot, parsnip, turnip, radish, salsify, of onion bulbs, hyacinth corms, cabbage heads, celery stalks and fruits of tomato, pepper and egg plant, also rot of lettuce, cauliflower, cucumber, muskmelon, potato, hyacinth and onion. In-

fection did not occur unless the epidermis was broken. The rotten mass was always soft, wet, and exuded a liquid clouded with bacteria.

Jones in 1909 made an extensive study of the cytolytic enzyme of this germ. This enzyme was separated by heat, filtration, formalin, phenol, thymol, chloroform, diffusion, alcohol, and its conditions of production and action investigated. Heating the enzyme to 60° inhibited its activity to a marked degree; higher than 63° inhibited it entirely; chloroform, thymol and phenol did not

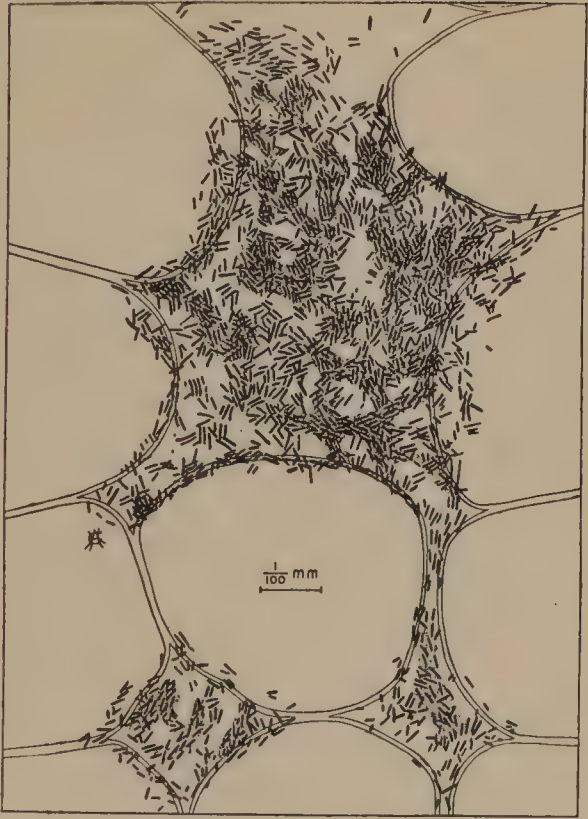


FIG. 31.—*B. carotovorus* wedging apart cells of the carrot. After Smith.



FIG. 32.—*B. carotovorus*. After Jones.

retard its action. No loss was suffered through alcoholic precipitation and resolution. The dried enzyme remained active for fully two years. Its effect was greatest at 42°, less at 32° and 48°. No diastatic action was observable.

In 1909 Harding and Morse, from an extended study of some 12,000 cultures of non-chromogenic, liquefying soft-rot bacilli of some forty-three pathogenic strains (including *B. carotovorus*, *B. oleraceæ*, *B. omnivorus*, *B. aroideæ* and what Potter regarded as *Pseudomonas destructans*), from six different vegetables, conclude that unless later studies of the pathogenicity of these cultures shall offer a basis for subdividing them, there is no apparent reason why they should not all be considered as somewhat variant members of a single botanical species.

This conception would lead to the abandonment of the supposed species mentioned above and the recognition of all of them under their oldest described form, *B. carotovorus* Jones, which in our present knowledge seems certainly to be the most wide spread, common and destructive of the soft rot bacteria. Some, perhaps much, of the rot of crucifers generally thought to be due to *Pseudomonas campestris* is probably caused by *B. carotovorus*.

B. coli (Esch.) Mig. or an organism indistinguishable from it was held by Johnston capable of causing rot of soft tissues of the cocoanut plant and to be responsible for cocoanut bud-rot.

B. lathyri Manns & Taubenhaus.¹

= *Erwinia lathyri* (M. & T.) Committee.

This organism is reported on sweet peas causing "streak." Brown spots appear on the stems and kill the cambium. Similar effects are produced on clover, bean and soy beans.

B. melonis Giddings which causes a rapid soft rot of muskmelons is very close to, perhaps identical with, *B. carotovorus*.

B. morulans Bonequet,² an organism with four long peritrichiate flagella, is found associated with beet curly-top but a causal relation to the disease has not been proved.

B. musæ Rorer.³

The vessels are filled with bacteria and a wilt of the plant is caused. Pathogenicity was proved by inoculation with pure cultures. The organism is recognized by the fact that it quickly becomes black on potatoes.

¹ Manns, T. F. A bacterial disease of the sweet pea and clovers. *Phytop.* **3**: 74, 1913.

² Bonequet, P. A. *Bacillus morulans* n. sp. *Phytop.* **7**: 269, 1917.

³ Rorer, J. B. A bacterial disease of bananas and plantains. *Phytop.* **1**: 45, 1911.

B. phytophthorus Appel

= *Erwinia phytophthora* (App.) Committee.

A non-sporiferous rod, $0.6-0.8 \times 1.5-2.5 \mu$, actively motile by peritrichiate flagella. Gram negative; aërobic or a facultative anaërobe; grayish white on agar; surface colonies round, smooth; gelatine liquefaction moderate; bouillon clouded; no indol; no gas. Nitrate changed to nitrite. Milk coagulated and casein precipitated. Opt. $28-30^{\circ}$. T. D. P. 47° .

It was described by Appel as the chief cause of potato black-leg. (See also p. 41.) The description given above, made from Appel's organism, is by E. F. Smith, who says this organism is not sufficiently distinguished from *B. carotovorus*. The parenchyma is chiefly affected, though the vessels are exceptionally occupied, by a soft rot both in the stem and tuber. Infection is chiefly intercellular.

B. solanisaprus Harr.

A bacillus with rounded ends, $1.5-4 \times 0.6-0.9 \mu$, variable in culture; actively motile by $5-15 +$ peritrichiate flagella; no spores seen. Gram negative. Gelatine colonies, punctiform 0.25 mm. at two days; gelatine stab filiform. Liquefaction noticeable on the thirty-fifth day. Agar colonies punctiform at two days, 1-5 mm., gray-white, slimy, flat. Bouillon turbid with fine sediment; ring, and thin band present; milk curdled. Gas only in mannite and lactose. Nitrate reduced to nitrite. Opt. $25-28^{\circ}$. T. D. P. 54° , 10 min.

It was found constantly associated with a type of potato disease which Harrison regarded as distinct from black-leg and from

the disease caused by *Ps. solanacearum*. It was repeatedly isolated from diseased tubers, stems and leaf veins and occurred in practically pure culture in freshly infected tissue.

The organisms first appeared in the ducts and thence invaded

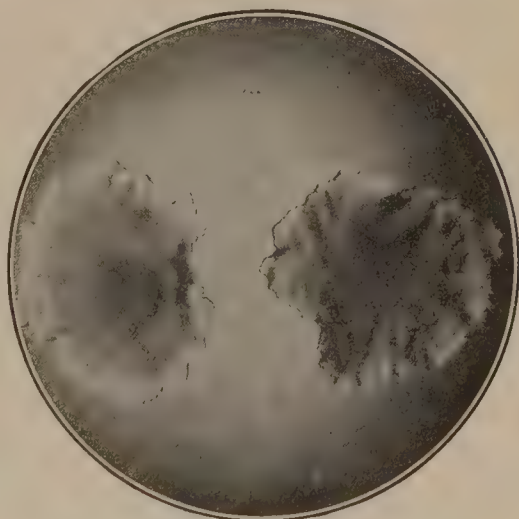


FIG. 33.—Surface colonies of *B. solanisaprus*.
After Harrison.

the surrounding tissue, dissolving the middle lamellæ and producing cavities. Inoculations of pure cultures into healthy plants

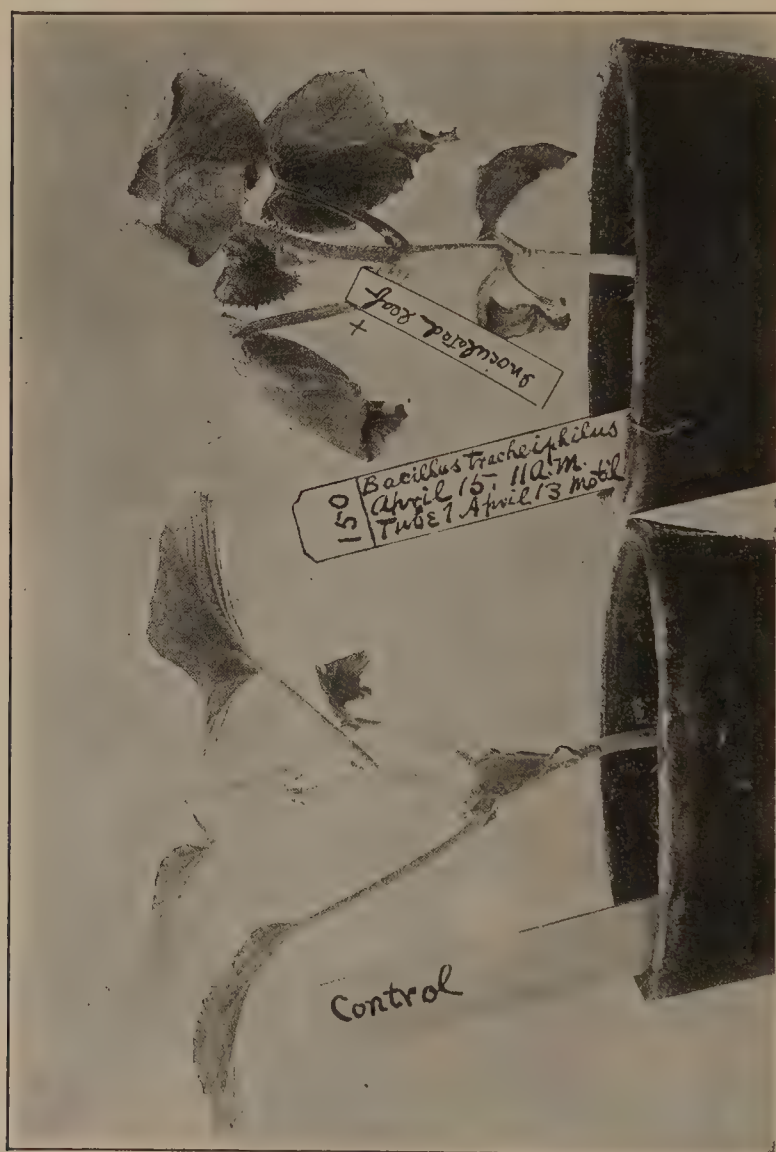


FIG. 34.—Muskmelon plant inoculated with a pure culture of *B. tracheiphilus*. After Smith.

produced characteristic lesions and the organism was re-isolated. Characteristic enzymic action was observed on placing precipitated enzyme on slices of potato.

B. tracheiphilus E. F. Sm.

= *Erwinia tracheiphila* (E. F. Sm.) Committee.

Bacillus 1.2–2.5 x 0.5–0.7 μ , variable, actively motile in young cultures; capsulated, no spores, flagella peritrichiate; no gelatine liquefaction. On agar thin, smooth, milk-white; no gas, aerobic or facultative anaerobic; milk not curdled. T. D. P. 43°, 10 min.

This pathogen is found filling the vessels of cucurbits, (musk-melons and cucumbers) affected with wilt. The disease has been produced artificially by puncture inoculations on the blades of leaves with the white sticky fluid from infected veins. The inoculated plants showed symptoms of wilt after four days and sixteen days later the ducts of the vine were found to be plugged with bacteria. The organism was then isolated from this artificially infected plant. The cultures thus obtained were carried by transfers over winter and in December were used successfully to infect cucumber plants. Control plants were never diseased.

The disease is transmitted by insects and gains entrance to its host through wounds.

Others have been reported on corn, ginseng, beet, onion, sugarcane, cherry, grape, hemp, lupine, calla, larkspur, dahlia, hyacinth, iris, orchids, rose, willow, poplar.

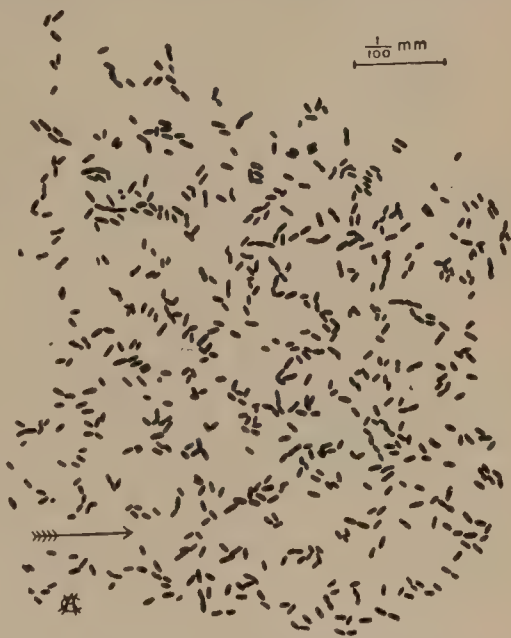


FIG. 35.—*B. tracheiphilus*. After Smith.

ACTINOMYCETALES (p. 14)

Actinomycetacæ

Actinomyces Harz.¹

Organism growing in form of a much-branched mycelium which may break up into segments that function as conidia. Non-motile.

Actinomyces scabies (Thaxt.) Güssow

= *Oospora scabies* Thaxt.

Gelatine liquifaction slow; growth on all media gray to buff with a dark gray aerial mycelium which consists of long prostrate filaments on which lateral branches are inserted at short intervals. Secondary branching abundant. Spores more or less cylindrical, $0.8-0.9 \times 1.3-1.5 \mu$, from dextrorse spiral hyphæ of 3-14 turns are developed richly on most media. On synthetic agar the growth



FIG. 36.—Surface view of cork cells showing the mycelium within. After Lutman.



FIG. 37.—Section of phellogen showing fat globules. After Lutman.

is abundant, cream-colored, chiefly on surface of medium, wrinkled, raised. The aerial mycelium is white, scarce, in some strains absent.

On nutrient agar the growth consists of round, entire, colonies, surface at first smooth, later raised, lichnoid, often becoming wrinkled; color white to straw, opalescent to opaque. Aerial mycelium usually absent. On potato plugs the growth is gray, opalescent, later turning jet black, wrinkled colonies covering all the plug, which also turns black.

It produces scab on potato and beet.

¹Waksman, S. A. Cultural studies of species of *Actinomyces*. *Soil Science* 8: 71, 1919.

The scab on the potato may originate at any place on the tuber, but frequently occurs at the lenticels. It is due to hypertrophy of the cells of the cork cambium, accompanied by hyperplasia. The walls of the hypertrophied cells are much thickened by suber-

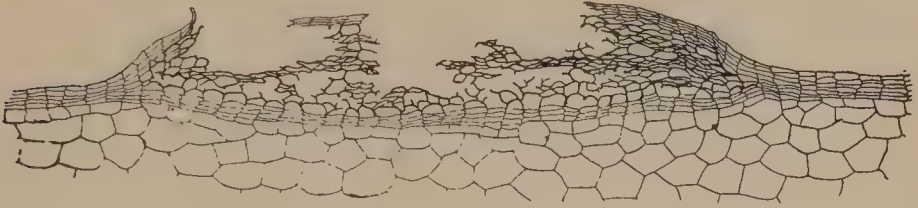


FIG. 38.—Drawing of a section of an old scab. After Lutman.

ization. The filaments of the fungus are formed in the cork cambium; and in the outer layers of the starch parenchyma fat instead of starch is present.

Less known bacterial plant diseases. The literature abounds in references to what are regarded as cases of plant bacteriose; cases which as yet rest upon very incomplete evidence. In many of these bacteria are found in abundance in the diseased tissue but pathogenicity has not been proved by inoculation nor pure cultures made.

DIVISION III

EUMYCETES. TRUE FUNGI (p. 2)

In general the true fungi are readily distinguished from the slime molds and bacteria by the presence of the mycelium; exceptions occur in the Chytridiales (p. 57) and the genus *Actinomyces* (p. 48).

The **Vegetative Body** is devoid of chlorophyll and is often hyaline though sometimes colored. Typically it consists of a more or less branched filament of apical growth, the **mycelium**. This mycelium



FIG. 39.—Showing a septate mycelium within host cells.
After Stevens and Hall.

may be cut into cells by partitions (**septa**) or may be **continuous**, i. e., without septa. The cells of the septate mycelium do not differ essentially from typical plant cells except in the absence of chlorophyll. They consist of masses of protoplasm, the **protoplasts**, bearing vacuoles and are more or less rich in oils, acids, gums, alkaloids, sugars, resins, coloring matter, etc., vary-

ing in amount and kind with the particular species and condition of the fungus. The protoplast is covered by a cell wall which consists of cellulose though often of a special quality known as **fungous cellulose**. The protoplast bears one or in some fungi two or more **nuclei**. The vacuolation of the protoplasm, the mode of branching of the cells, their color, and dimensions, are in some cases quite characteristic.

In one class, the Phycomycetes, the active vegetative mycelium

possesses no septa except such as serve to cut off the sexual or other reproductive organs or such as are found in senility. The protoplasm is therefore continuous throughout the whole plant body and may be regarded as constituting one cell though it may be of great extent and bear very numerous nuclei. Such multinucleate cells, **coenocytes**, may be regarded as cell complexes with the walls omitted.

In one comparatively small order, the Chytridiales, there is often no filamentous mycelium and the vegetative body consists merely of a globular, irregularly spherical or amoeboid cell.

Reproduction. Vegetative. Small sections of mycelium if placed in suitable environment; that is, if supplied with food, moisture and warmth will continue to grow, soon equaling the parent mycelium in size. Bits of diseased tissue, bearing mycelium, thus constitute ready means of multiplication and dispersal.

Asexual Spores. A spore is a special cell set aside to reproduce the plant. An asexual spore is a spore not produced by a sexual process. Manifold forms of asexual spores exist among the fungi.

In some of the simplest cases, budlike out-growths (**gemmæ**) appear on the mycelium; or portions of the mycelium itself are cut off by partitions and the protoplasm inside gathers into a mass and protects itself by a firmer wall than that of the mycelium, **chlamydospores**.

In other cases special branches, **hyphæ**, are set apart for the purpose of bearing spores. If the spores are cut off from the tip of the branch they are known as **conidia** or **conidiospores**, and the branch bearing them is a **conidiophore**. Conidia may be borne singly or in false clusters caused by the young pushing the older conidia aside; frequently they are produced in chains, **catenulate**, Fig. 40, owing to the development of one spore below another

before the elder spore is shed. Conidia may be either **simple**, composed of one cell, or **compound**, composed of two or more cells. In compound spores each cell is at least potentially a spore and can germinate under favorable conditions and perpetuate the species. In many compound spores the germinating function is sacrificed by one or more of their component cells.

Conidiophores may consist of loosely branching, rather long,



FIG. 40.—One form of conidium. *Oidium*. After Biolotti.

superficial hyphæ, or they may be short, innate, and in close clusters forming distinct spore bearing spots. Figs. 335, 337. Such sporiferous spots when naked are called **acervuli**. Often the conidiophores are roofed over with a net-work of woven fungous threads thus constituting a special spore bearing structure, the **pycnidium**.



FIG. 41.—Conidia borne in a pycnidium. After Quaintance and Shear.

Fig. 41. Conidiophores may be solitary or grow together in bundles, Figs. 390, 391, or branch loosely as in Fig. 351.

The **basidium**, Fig. 42, is a special kind of sporophore bearing at its apex usually four, sometimes two, small projections, **sterigmata**, each of which produces one spore, for distinction called a **basidiospore**.

Some fungi bear the spores loose inside of the swollen tips of sporophores as in Fig. 74. The spore bearing structure is then called a **sporangium** and its stalk a **sporangiophore**. The

ascus is another spore bearing structure. In it the spores are borne very much as they are in the sporangium but usually of definite number, 1, 2, 4, 8, 16, etc., eight being the most common number. Asci may be naked or covered, scattered or collected in groups. When covered, the chamber in which they are borne is called a **perithecium**, Fig. 43; when on an open disk the disk is called an **apothecium**, Fig. 109.

According to their length of life spores are classed as: 1. **resting spores** whose function is to tide over unfavorable conditions, hence the common name "winter spore," and in contradistinction, 2. "summer spores" which are produced in abundance in warm weather, germinate immediately, and can ordinarily live but a short time.

In some species the spores that are to function in water possess

cilia, and the power of motion. These are **zoöspores** or **swarm spores**, Fig. 54.

At sporing time many kinds of fungi produce special structures for the bearing of spores. The fungous threads interweave to form a firm, or even a densely solid, mass and constitute a **false parenchyma**. Such are the stalks and caps of the mushrooms and of the shelving toadstools, the skin of the puffball, etc. A cross section of such a structure appears much as a true parenchyma, a longitudinal section shows it to be merely a mass of interwoven fungous threads.

Sexual Spores are formed by the union of sexual elements, **gametes**. They are most conspicuous among the Oömycetes where the **antheridium**



FIG. 42.—Basidia of various ages. After Schenck.

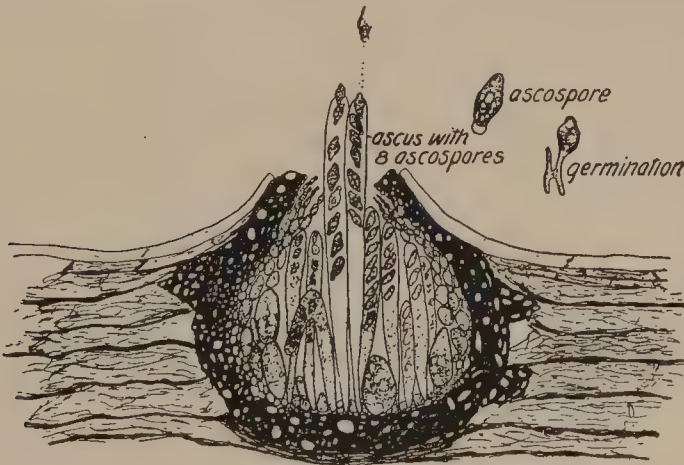


FIG. 43.—A perithecium with asci. After Reddick.

carries the **sperms** into the **oögonium**, fertilizes the **oösphere** and produces an **oöspore**. Fig. 61.

As a rule the sexual spores are produced toward the end of the

vegetative period of the fungus. The asexual spores are produced earlier and for a longer period. Sexual spores are commonly resting spores.

Germination of spores. Under suitable environment mature spores germinate and eventually give rise to vegetative bodies similar to that of the parent. The usual mode is for the mycelium to rise directly from the spore. In other instances the spores produce zoöspores which migrate, come to rest, then develop a mycelium. In still other cases a short mycelium, **promycelium**, is formed and from this small conidia, **sporidia**, develop. Fig. 237. These conidia give direct rise to the mycelium. Spores of some species may by gemmation lead a more or less prolonged existence without return to the mycelial stage.

Heat and Moisture Relation. Like all living things these organisms cannot develop without heat and moisture. The necessary degree of each varies with different species. In general the fungi that cause plant disease grow best at ordinary temperature conditions and therefore are cultured better at room temperature than at animal body temperature so often requisite for parasites of animals. Some species are strictly aquatic, and must be surrounded with water; others can grow in comparatively dry situations. Generally speaking, however, dampness favors fungous development, and the growth of most fungi is more vigorous in damp atmosphere. Humidity and warmth combined are proverbial as producers of mold and mildew. So conspicuous is the coincidence of these conditions with fungous growth, that in the minds of many a warm damp air is the cause rather than the condition of fungous development.

Respiration with the fungi as with all plants and animals consists in oxidation, involving intake and consumption of oxygen accompanied by the giving off of carbon dioxide and water, and since no photosynthesis occurs, this process is never masked as it is in the case of the chlorophyll-bearing plants.

In nutrition requirement there is great diversity; but in all cases carbon must be taken from some organic source. Starch, sugar, cellulose and kindred compounds are frequent sources of the carbon food supply. Nitrogenous foods are, generally speaking, not required in such abundance by the Eumycetes as by the bacteria and advantage may frequently be taken of this fact in isolating the fungi from bacteria by growing on media poor in nitrogen, in which case the fungi often outgrow the bacteria.

The color of the fungi is determined to some extent by the constitution of the media upon which they grow, but certain colors are also characteristic of certain groups, some are typically hyaline, others brown, others red, green, etc.

Many fungi exhibit a peculiar heterœcism, that is, part of their life cycle is passed through upon one host, part of it upon another host, even of very distant botanical kinship. Thus among the rusts; in one instance part of the life cycle passes upon the apple, the remainder upon the cedar tree. Fungi also exhibit **polymorphism**, i. e., in one stage they exhibit one spore form and in another stage another spore form totally different. In this way several apparently quite distinct types of spores and sporiferous structures may belong to the same species.

The mycelium is the vegetative part of the fungus and grows over or within the host tissues drawing its nourishment from the host cells and thereby rendering them diseased. Bits of tissue attacked by fungi, if teased apart, usually reveal under the microscope an abundance of mycelial threads. If these be constantly present, of one kind only, and no other parasites are present the presumption is that this mycelium is the cause of the disease.

Certain fungi (parasites) grow only in living hosts, others (saprophytes) in dead organic matter. Some mycelia merely grow between or within the host cells abstracting nutriment and water from the live cells. Some produce hypertrophy or hyperplasia resulting in large distortion. Others produce toxic substances which kill single cells or tissues. Still others produce enzymes that dissolve either the middle lamellæ or the cellulose walls and the affected part becomes soft and rotten.

Classification of Fungi. The true fungi in themselves constitute a very large group made up of diverse forms, many of which are as yet little known. Any satisfactory system of classification is impossible until much more knowledge obtains regarding their morphology, cytology, life histories and especially the relation to their hosts. According to present knowledge they comprise very numerous species distributed in three classes as follows:

KEY TO CLASSES OF **Eumycetes**

Mycelium continuous in vegetative stage.....	Class 1. Phycomycetes , p. 56.
Mycelium septate.....	Class 2. Ascomycetes , p. 87.
Spores in asci.....	

- Spores on basidia * Class 3. **Basidiomycetes**, p. 210.
 Not as above; spores on conidio-
 phores, naked, or in pycnidia;
 or spores quite unknown Fungi Imperfecti, p. 331.

Class I. **Phycomycetes**, Alga-like Fungi (p. 55)

The **Phycomycetes** are characterized by the absence of septa in the mycelium except in sporing branches, where they occur to cut off the spore-bearing cells or the gametangia, and in old filaments. The body is multi-nucleate and sexual spores as well as asexual ones are usually, though not always, produced. Some of the **Phycomycetes** live in water and possess zoöspores, others are parasitic on land plants and bear conidia or sporangia. These may germinate either by germ tubes or by zoöspores. The characteristic fertilization consists of a union of two gametes which may be like in character (**isogamy**) or unlike (**heterogamy**). If the sexual organs are unlike the receptacle which bears the sexual spores is called the **oögonium**, its eggs before fertilization **oöospheres**, and the spores **oöspores**. The receptacle bearing the fertilizing gamete is the **antheridium**, and the fertilizing elements are the **sperms**. In some forms which, by their sexual or asexual spores, show relation to the **Phycomycetes** the mycelium is wanting and the vegetative body is reduced to a single spherical or amoeboid cell, which frequently lives in a purely parasitic manner entirely imbedded in the protoplasts of its host. This mode of life constitutes the strictest kind of parasitism inasmuch as the fungus derives its nourishment from the still living host cell.

KEY TO ORDERS OF **Phycomycetes**

- Sexual spores when present heterogamous Subclass I. **Oömycetes**, p. 57.
 Mycelium poorly developed, frequently reduced to a single cell. Fruiting mycelium a single cell, or a group of cells in a sorus, forming either asexual resting spores or sporangia from the entire protoplasmic mass 1. **Chytridiales**, p. 57.
 Mycelium well developed 2. **Peronosporales**, p. 62.
 Sexual spores isogamous, formed by the union of similar gametes Subclass II. **Zygomycetes**, p. 83.
 Asexual spores several, in sporangia 3. **Mucorales**, p. 84.

* In the rusts and smuts the promycelium is regarded as a basidium.

Subclass **Oömycetes** (p. 56)

In the Oömycetes there is pronounced difference between the male and female sexual organs. The oögonium is comparatively large, and contains one or more large passive eggs (oöspheres), which are fertilized by sperms, differentiated or not, which either swim to the oögonium by cilia, creep to it, or are carried to it by a fertilizing tube. Oöspores are in some species produced frequently and abundantly while in others they are entirely unknown. The asexual reproduction is by either conidia or sporangia.

Chytridiales^{1, 2} (p. 56)

The members of this order are the simplest of any of the Phycomyces. Many of them are single, more or less globose, undifferentiated cells, others have a more or less prominent haustorium-like mycelium, while but few have any approach to a true mycelial development. Most are intracellular parasites; a few of the more highly developed genera are intercellular parasites. With few exceptions reproduction is entirely asexual, all spores being formed directly from the vegetative cell. Zoösporangia and thick-walled resting spores are produced. The zoöspores have either one or two cilia. There are over forty genera and two hundred species. The majority of the species are inconspicuous parasites of algæ and infusoria; but some genera, like *Synchytrium*, *Physoderma* and *Urophlyctis*, produce conspicuous sori and large hypertrophy of land plants.

Examination of dead material of any of the Chytridiales usually discloses but little; for purposes of classification, the life history, mode of formation of sporangia and zoöspores, must be ascertained.

KEY TO FAMILIES OF Chytridiales

- Spores all asexual, or rarely formed by the union of free-swimming gametes
 Mycelium none, sporangia grouped into sori..... 1. **Synchytriaceæ**, p. 58.
 Mycelium present, of delicate, extended, evanescent, haustoria-like strands; sporangia terminal or intercalary..... 2. **Cladochytriaceæ**, p. 60.
 Spores both sexual and asexual, gametes heterogamous..... 3. **Oöchytriaceæ**, p. 61.

¹ Lüdi, R. Beiträge zur Kenntniss der Chytridiaceen. Hedw. **40**: 1, 1901.

² Rytz, W. Beiträge zur Kenntniss der Gattung *Synchytrium*. Cent. Bact. II, **18**: 635, 1907.

Synchytriaceæ¹ (p. 51)

The infecting zoöspore invades the host cell and becomes parasitic upon the still living protoplasm. Hypertrophy of this and adjacent host cells is usually induced, resulting in the formation of a small gall around the infected cell. This gall is often colored and bears a superficial resemblance to a rust sorus. The parasite enlarges until it occupies nearly the whole of the host cell. In *Synchytrium* the one nucleus then enlarges and divides to produce numerous nuclei. The whole mass then divides into segments regarded as sporangia, and each sporangium divides into numerous uninucleate parts, each of which develops into a zoöspore. In some species development is arrested before the division of the primary nucleus; the protoplast becomes spherical, invests itself with a thick wall and becomes a resting spore. (Fig. 44.) After a more or less protracted period of rest zoöspores develop.

The family includes some fifty species, all of which, except those of two small genera, are parasitic upon land plants.

***Synchytrium* de Bary & Woronin**

Zoösporangia formed by division of an initial cell to form a sorus of sporangial cells; sporangia formed directly from the full-grown plant body.

Upon reaching maturity the plant body develops directly into a sporangial sorus. Both zoösporangia and winter spores are present.

S. endobioticum (Schilb.) Perc.,² the cause of a very serious wart disease of the potato, was originally described as *Chrysophlyctis endobioticum* by Schiliberzky in Hungary in 1896, and transferred to *Synchytrium* by Percival. It invaded America about 1909.

In summer the resting sporangia, which average about 52 μ in diameter, are found in abundance in the host cells near the surface, few in the outer layer, more below, down to the sixth or eighth row of cells. Each resting sporangium contains several hundred roundish zoöspores which measure 2–2.5 μ . In spring the resting sporangia germinate, freeing numerous, pear-shaped, uniciliate zoöspores. Another type of sporangium consists of thin sacs, pro-

¹ Tobler-Wolf, G. Die Synchytrien. Archiv. f. Protistenkunde. **28**: 14, 1913.

² Curtis, K. M. The life-history and cytology of *Synchytrium endobioticum* (Schilb.) Perc., the cause of wart disease in potato. Phil. Trans. Roy. Soc. London. **210**: 409, 1921.

duced singly or two to five in a sorus, each bearing numerous zoöspores or gametes.

The zoöspores infect the potato in bud tissue of rhizomes and in the "eyes" of young tubers. Usually only one zoöspore enters each cell but occasionally more may do so. General division of cells, neighbors to the infected cell, occurs, resulting in a tumor. The epidermal cells surrounding the infected cells grow up to form rosettes overarching the host cells at their bases. By division of an infected epidermal host cell the diseased cell may become deeply placed in the tumor. The zoöspore after entering the host cell enlarges and after repeated nuclear mitoses, segments to form about five thin-walled sporangia, which constitute the sorus; after more mitoses zoöspores, sometimes gametes, are formed. Eventually the host cell dies and its con-

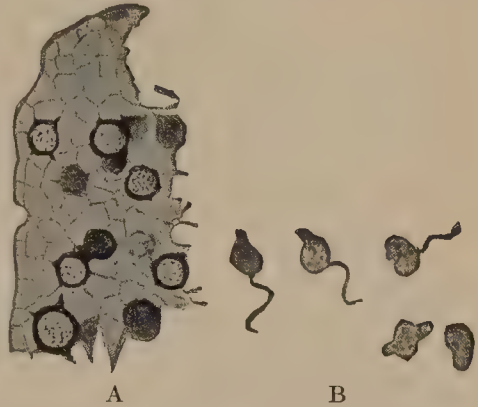


FIG. 44.—A, section showing sporangia or sporocysts; B, zoöspores, ciliated and amoeboid. After Percival.



FIG. 45.—*S. endobioticum*. Division of an epidermal host cell with parasites in its lower part. After Curtis.

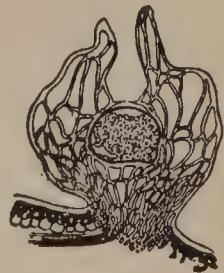


FIG. 46.—Gall of *S. vaccinii*. After Shear.

tents are deposited as a brown episporium upon the parasite. The zoöspores at maturity are liberated by rupture of the soral envelope.

Crushed sporangia produce characteristic warts in three to four days when placed on susceptible parts.

S. vaccinii Thomas is the cause of a disease of the cranberry and related hosts. It forms numerous small, reddish galls in which, deeply embedded, are the sori.

Cladochytriaceæ (p. 57)

A branching mycelium runs through or between the cells of the host drawing nourishment from many cells. Sporangia are either apical or intercalary and contain uniciliate zoöspores. Resting spores are also produced. There are about a half dozen genera and some thirty species.

Physoderma Wallr.

P. zeæ-maydis Shaw

Thick-walled, smooth, brown, resting spores, sporangia, 18–24 x 20–30 μ , each with one side slightly flattened and showing the definite outline of a cap or lid, are found in great numbers within the diseased tissues. The mycelium, consisting of very fine (1μ) fibers (Fig. 47), connects the large vegetative cells which occur singly or in groups, and is no longer ap-



FIG. 47.—*P. zeæ-maydis*. A host cell showing parasite within. After Tisdale.

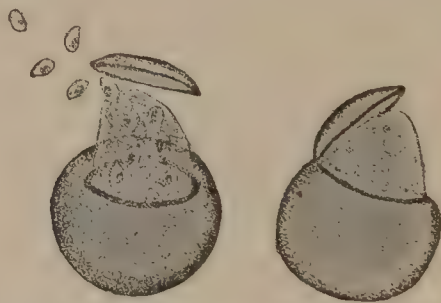


FIG. 48.—*P. zeæ-maydis*. Sporangium showing mode of opening; emerging zoöspores. After Tisdale.

parent when the spores are mature. In germination the lid of the resting spore opens, door-like, (Fig. 48) and soon the uniciliate zoöspores, 20–50 in number, emerge.

The zoöspores soon lose their cilia, become amoeboid and germinate by sending out very fine hyphæ which penetrate into the epidermal cells. Penetration continues, the fine mycelium invading a number of surrounding parenchyma cells and within producing groups of enlarged cells. Some of these enlarged cells develop

directly into sporangia and the mycelium disappears. Affected cells then die. Thus large dead spots are produced on the leaves, sheaths, and stalks. On corn. Teosinte is also susceptible.

This fungus was discovered in India by Shaw in 1910 and in Illinois by Barrett in 1911.

Oöchytriaceæ (p. 57)

The plant body is either an undifferentiated cell or a well developed mycelium; reproduction by means of asexual swarm spores and sexual resting spores. Only one genus is of economic importance.

Urophlyctis Schröter

Mycelium endophytic, producing zoösporangia on the surface of the host and thick-walled oöspores within the tissues; zoöspores uniciliate. The genus contains some half dozen species, all of which are parasitic on higher plants.

U. alfalfæ (Lagerh.) P. Mag.¹

On Alfalfa causing galls.

Infection is by zoöspores and turbinated bodies are produced within the epidermal cells and attached by a beak, Fig. 49. This

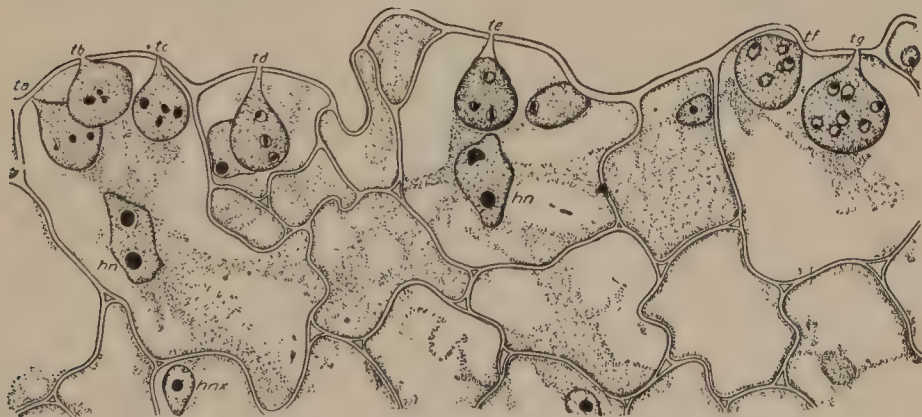


FIG. 49.—*U. Alfalfæ*. Section of epidermis showing primary turbinated cells, ta, tb, etc., each with several nuclei. After Jones and Drechsler.

body, at first uninucleate, becomes multinucleate and by septation and branching brings about a structure such as is shown in Fig. 50, new series of turbinated cells being formed on the ends of delicate

¹Jones, F. R. and Drechsler, C. Crown wart of alfalfa caused by *Urophlyctis alfalfæ*. Jour. Agr. Res. **20**: 295, 1920.

(0.5-1 μ) mycelial filaments and resting spores forming on the turbinated cells. The resting spores are the most conspicuous structures found on dissection of diseased tissue and are yellow, brittle, about 40 μ in diameter and with a thick (1.5 μ) wall. The haustoria disappear on old resting spores. The fungus primarily attacks the very young leaf scales and leaves of the bud. The in-

vaded cells and the adjacent cells undergo hypertrophy, producing galls. The walls of the host cells are dissolved before the advance of the fungus producing large cavities.

Other species are on beets, *Chenopodium*, *Atriplex* and clover.

Peronosporales (p. 56)

The mycelial threads in most strictly parasitic forms wander between the host cells and draw nutriment from them by short branches, sucking organs, **haustoria**, (Fig. 60) of various forms, which penetrate into the victimized cell. Two kinds of spores are produced, sexual and asexual. The sexual spores result from the union of two unlike gametes, the egg (oosphere) and sperm, borne respectively in the oögonium and antheridium. Each oögonium bears a solitary oosphere. Fertilization is accomplished by means of



FIG. 50.—A later stage in the development of *U. alfalfæ*, ta, tb, turbinated cells, ra, resting spore. Haustoria are seen on the tips of the turbinated cells and encircling the resting spore. After Jones and Drechsler.

a tube from the antheridium and penetrating into the oögonium. The sexual spores are thick-walled, resistant, and usually require a long time to reach maturity. They are, therefore, often called "resting spores." In germinating the sexual spores produce either germ tubes or develop directly into zoösporangia. The asexual spores are conidia. They are borne on conidiophores which arise from the mycelium and which may be short or long, simple or branched, subepidermal or superficial according to the habit of the species. The conidia in various genera germinate by three methods, (1) a germ tube is sent out by the conidium, (2) the en-

tire protoplasmic contents of the spore passes outside the spore wall and then forms a germ tube, or (3) the conidium by internal division breaks up into zoöspores.

KEY TO FAMILIES OF *Peronosporales*

- Conidiophores poorly defined or of sympodial development 1. *Pythiaceæ* p. 63.
 Conidiophores not as above
 Conidiophores, short, thick, subepidermal, conidia catenulate 2. *Albuginaceæ*, p. 70.
 Conidiophores, longer, superficial, simple or branched, conidia not catenulate 3. *Peronosporaceæ*, p. 73.

Pythiaceæ ¹

This family shows affinity with both the *Peronosporales* and the *Saprolegniales* and is sometimes classed with one, sometimes with the other.

- Zoöspores differentiated outside of the zoösporangia 1. *Pythium*, p. 63.
 Zoöspores usually differentiated within the zoösporangia
 Fertile mycelium delicate 2. *Pythiacystis*, p. 65.
 Fertile mycelium robust 3. *Phytophthora*, p. 66.

Pythium Pringsheim ² (p. 63)

The mycelium is found in abundance in and about the infected tissue as fine, branched, continuous threads. These, in the terrestrial species, bear conidia on branches which are of the same character as the mycelium itself. The conidia germinate either by a rupture of the wall or by the formation of a beak-like process through which the protoplasm is extruded, after which it becomes differentiated into zoöspores. Gemmæ, very like the conidia in appearance, are also produced.

The oögonia are quite like the conidia and gemmæ in structure, but develop oöspores within. The oögonium is at first multinucleate but as the oösphere matures all of the nuclei except one migrate toward the periphery, the periplasm, or degenerate in the

¹ Fitzpatrick, H. M. Generic concepts in the *Pythiaceæ* and *Blastocladiaceæ*. *Mycol.* **15**: 166, 1923.

² Butler, E. J. An account of the genus *Pythium* and some *Chytridiaceæ*. *Mem. Dept. Agri., in India, Botanical series* 1, no. 5; 1, 1907.

öoplasm, resulting at maturity in an uninucleate egg. This is fertilized by one nucleus from the antheridium. No sperm is differ-



FIG. 51.—Cucumber seedlings. Pots 5, 6, and 8 inoculated with *Pythium*. Pot 7, Control. After Atkinson.

entiated, and the contents of the antheridium are carried over to the egg by a fertilizing tube. Members of the genus are aggressively parasitic only under most favorable environmental conditions of heat and moisture.

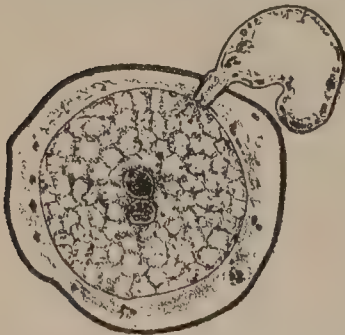


FIG. 52.—Fertilization in *Pythium*, showing oögonium, antheridium, oöspore, periplasm and the ♂ and ♀ nuclei. After Miyaki.

P. debaryanum Hesse¹ is most common as the cause of "damping off."

Zoösporangia or "conidia" globose to elliptic, usually papillate, 20–25 μ ; gemmæ similar in form and size; oöspores globose, hyaline, smooth, 15–18 μ .

It is also recorded as the cause of "leak," a rapid soft rot, of the Irish potato.

Studies have shown that *P. debaryanum* destroys pentosans, starch and sugar in potato tubers. It secretes a toxin which kills the cells, also an enzyme that dissolves

¹Hawkins, L. A. and Harvey, R. B. Physiological study of the parasitism of *Pythium debaryanum*. Hesse on the potato tuber. Jour. Agr. Res. 18: 275, 1919.

the middle lamella. It is claimed that the cell walls are penetrated by mechanical pressure. Fig. 53.

***P. aphanidermatum* (Edson) Fitzpatrick**

Mycelium $2.8-7\ \mu$; presporangia terminal, clavate or branched, $50-1000 \times 4-20\ \mu$, sporangia becoming spherical on release, then cleaving into zoöspores which are plano-convex and biciliate, $12 \times$

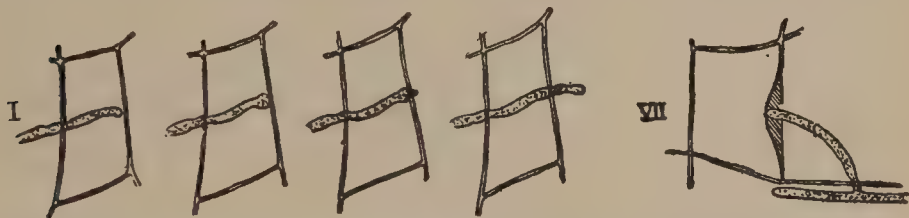


FIG. 53.—Drawings showing mode of penetration of potato-cell walls by *Pythium*: I Swelling of the hypha on contact, followed by penetration by a small tube. VII showing bending of wall by hyphal pressure. After Hawkins and Harvey.

$7.5\ \mu$; oögonia terminal, spherical, $22-27\ \mu$; oöspores single, $17 \times 19\ \mu$. The cause of “damping off” in beets and of black-root of radish.

Other species occur on ferns, ginger and palm.

***Pythiacystis*, Smith & Smith (p. 63)**

The sporangiophore is delicate, septate, and bears numerous sporangia sympodially. These produce many biciliate zoöspores internally. No oöspores have been seen. Only one species is known, and this of close kinship with *Phytophthora*.

***P. citrophthora* Sm. & Sm.**

Parasitic on lemons, the sterile mycelium inhabiting the rind; spores normally formed in the soil near infected fruits; sporangia ovate or lemon-shaped, papillate, $20-60 \times 30-90\ \mu$, averaging $35 \times 50\ \mu$, borne sympodially; zoöspores $10-16\ \mu$, at first elongate, becoming rounded and bearing two lateral cilia.

Infection by pure cultures prove that the fungus is the true cause of the rot. Gummosis, in which the dead bark remains hard, is also caused on lemon twigs by this fungus.



FIG. 54.—*P. citrophthora*; development of swarmspores from sporangia. After Smith and Smith.

Phytophthora de Bary^{1, 2} (p. 63)

This genus is of especial interest on account of its one exceedingly destructive representative, *P. infestans*, which occupies an historic position in phytopathology as one of the earliest of parasitic fungi to receive study in any way complete or adequate; study moreover which did much to turn attention and interest toward plant pathology.

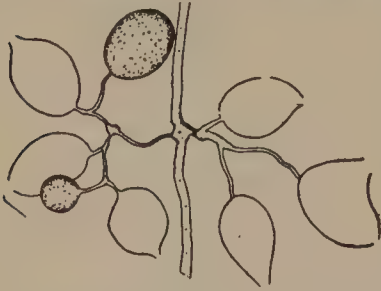


FIG. 55.—Sporangiophores and sporangia of *Pythiacystis*. After Smith and Smith.

In most species the conidiophores have irregular thickenings below the apparently lateral conidia. The conidiophore is at first simple and bears a single apical conidium after the production of which a lateral branch arises below the conidium and grows on in such a way as to give the first conidium a lateral appearance. This process is, in some species, repeated until a scorpioid cyme is produced. The mycelium is much branched, non-septate, hyaline; the conidiophores arise singly or in groups from the stomata, or break through the epidermis; conidia oval, papillate; zoöspores oval, biciliate, escaping by rupture of the papilla; oöspores, when present, with the episporium more or less ridged. The mycelium characteristically lives in and between the dead cells, not in the live cells of the host.

***P. phaseoli* Thaxt.** Mycelium well developed, intracellular; conidiophores single or in clusters from the stomata, simple or branched below, apparently simple above but really one to many times cymosely branched; conidia oval or elliptic, papillate, $35-50 \times 20-24 \mu$; germination by about fifteen zoöspores. Oögonia in the seed coats or cotyledons of seeds, rarely in the pods, thin walled, slightly folded, subspherical, $23-28 \mu$; oöspores spherical or subspherical with smooth, moderately thick walls, hyaline or light yellow, $18-26 \mu$. It was de-

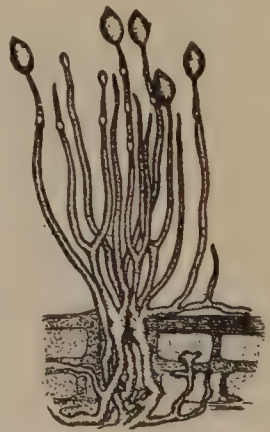


FIG. 56.—Structural details of *P. phaseoli*. After Thaxter.

¹ Wilson, G. W. A review of the genus *Phytophthora*. *Mycol.* **6**: 54, 1914.

² Rosenbaum, J. Studies of the genus *Phytophthora*. *Jour. Agr. Res.* **8**: 233, 1917.

scribed on lima beans in 1889. The methods of infection were studied by Sturgis who showed that spores are carried to the basal portion of the style and ovary by visiting insects. Oöspores were described, and extensive artificial culture experiments made, by Clinton who first grew the fungus successfully in pure culture on corn-meal agar and other media.

The species is unique within the genus on account of the single conidia which are borne at the apex of apparently simple conidiophores but subtended by several enlargements of the kind so characteristic of the genus.

P. infestans (Mont.) de Bary

Mycelium well developed; conidiophores single or in groups of 2-4 from the stomata; scorpiose-cymosely branched; conidia 27-30 x 15-20 μ , ovoid; germinating by about six to sixteen zoöspores.

On solanaceous hosts, particularly the potato and tomato, this species is very destructive. It was first described in 1845 as a *Botrytis* and has since been the subject of many extensive papers.

The conidiophores are abundant on the lower sides of infected leaves near the invasion line. The mycelium migrates between the cells piercing them with haustoria.

The existence of oöspores was a much controverted point; the structures first reported as oöspores probably belonged to some other fungus. Within recent years Clinton has obtained in pure cultures perfect oögonia, antheridia and oöspores.

In germination the conidia give rise to oval, flattened, biciliate zoöspores which emerge, come to rest, develop a wall, and then produce a germ tube. Direct germination by a germ tube also occurs rarely. Infection is brought about by the germ tube, either penetrating through stomata or directly through the epidermis.

The walls and contents of parasitized cells are browned. This fungus alone on tubers induces dry rot, but invasion of numerous saprophytic fungi and bacteria usually turns this into a disagreeable wet rot. Tuber infection occurs largely from conidia washed

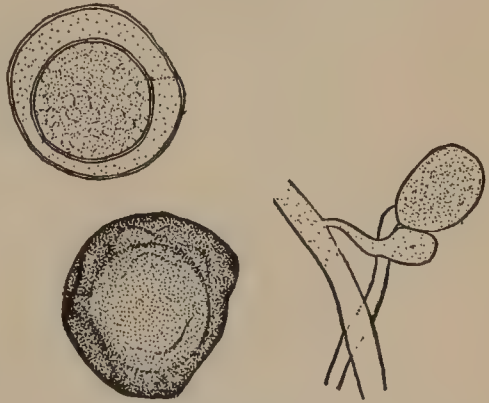


FIG. 57.—Young and mature oöspores of *P. phaseoli*. After Clinton.

into the soil by rain; possibly sometimes by the mycelium migrating by way of the stem.

The fungus in pure culture was extensively studied by Jones and



FIG. 58.—*P. infestans*; 1, section showing conidiophores and conidia formation; 5, germination of conidia. After Scribner.

a decided difference in luxuriance of growth was observed on blocks cut from different varieties of potatoes.

Hibernation occurs in part, at least, in live mycelium in infected tubers. The conidia are short-lived especially when dry.

P. omnivora de Bary. Conidiophores simple or branched; conidia ovoid or lemon-shaped, 50–60 or even 90 x 35–40 μ , germinat-

ing by as many as fifty zoöspores; oöspores smoothish or wrinkled, light-brown, transparent, $24-30\ \mu$. This species is found upon seedlings of some fifteen families ranging from Pines to the higher Angiosperms.

P. parasitica Dastur. var. **rhei** Godfrey.¹

Mycelium at first continuous, later sparingly septate; $5-15\ \mu$ in diameter, mostly intercellular, producing haustoria which may be small and subspherical, or finger-like; sporangiophores not distinguishable from the mycelium; sporangia usually terminal, normally ovate and papillate, mostly $24-35 \times 36-48\ \mu$, germinating by zoöspores or rarely by germ tubes; zoöspores biciliate, $8-9 \times 11-13\ \mu$, becoming globoid; chlamydospores globose, $27-42\ \mu$, walls thick; oögonia abundant in old cultures, $24-33\ \mu$ in diameter, pale to brownish; antheridia variable; oöspores globose, thick-walled, mostly $24\ \mu$ in diameter; profuse on most vegetable culture media.

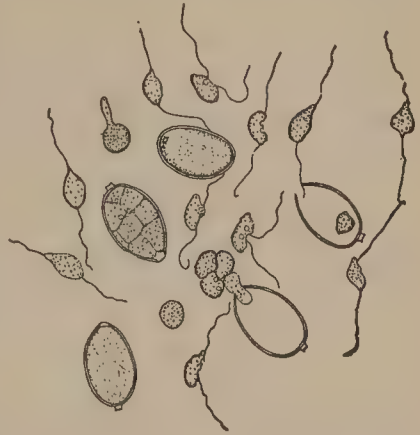


FIG. 59.—Formation of swarm-spores of *Phytophthora*. After Smith.

Parasitic in the base of leaf petioles and roots of rhubarb causing rot followed by sudden wilting of the foliage. The fungus advances from the leaf base into the root causing a brown decay. Death of all the leaves and of the plant may result.

P. cactorum (Lib. & Cohn) Schr. also causes a rot of rhubarb,² in general much like that described above though the fungus is adapted to lower temperatures and therefore is less injurious in hot weather, although there is little difference in the ultimate damage caused by the two. The fungus usually enters through wounds; the mycelium is intercellular with haustoria.

This fungus occurs also on apples, pears, tulip and ginseng.

P. terrestria Sherbakoff

Mycelium at first continuous then septate; conidia usually terminal, mostly oval, $36-46 \times 24-35\ \mu$, germinating mostly by

¹ Godfrey, George H. A *Phytophthora* footrot of rhubarb. Jour. Agr. Res. **23**: 1, 1923.

² Beach, W. S. A crown rot on rhubarb caused by *Phytophthora cactorum*, Pa. Agr. Exp. Sta. Bul. 174, 1922.

swarm-spores; swarm-spores asymmetric, with two cilia on one side, 9–11 μ when in resting globoid stage; chlamydospores common, mostly globose, 30–40 μ ; oögonia common in old cultures on steamed bean pods, globose, 19–24 μ ; oospores globose, 18–21 μ ; colonies on corn-meal agar, tufted.

Parasitic in tomato fruit causing buckeye rot; in bark of trunks of citrus trees causing foot rot; in stems of Lupine causing stem rot.

P. capsici Leonian ¹

Sporangiophores branched; sporangia generally ovoid, varying in culture to ellipsoid, subspheroid or irregularly elongate; papilla very prominent, germination normally by zoöspores, under special conditions by germ tubes; size of sporangia variable, 35–85 or even 105 x 21–56 μ ; oöspores formed on submerged mycelium, abundant on oat-meal and corn-meal agars, slightly wrinkled, brown, semi-transparent, 25–35 μ ; antheridia basal; no chlamydospores observed. Parasitic on stems and fruit of pepper.

Other species are on lilac, tobacco, colocasia, Agave.

Albuginaceæ ² (p. 63)

There is a single genus, **Albugo** (Persoon) Roussel,² of about fifteen species entirely parasitic upon flowering plants, causing the "white rusts." The conidia are borne in white blister-like sori under the raised and finally ruptured epidermis of the host. The conidiophores are short, club-shaped, arranged in clusters; the spores are borne in basipetal succession and remain attached in rather long chains unless disturbed.

The mycelium is very fine, intercellular, obligate parasitic, and penetrates the cells by globular haustoria. The rudimentary oögonium is multinucleate and filled with uniform protoplasm. As the oögonium grows older the protoplasm within differentiates into two parts, the inner part of dense protoplasm, the oösphere, and the outer part less dense, the periplasm. Figs. 61, 63, 64.

¹ Leonian, Leon, N. Stem and fruit blight of peppers caused by *Phytophthora capsici* Sp. Nov. *Phytop.* **12**: 403, 1922.

² Wilson, G. W. Studies in North American Peronosporales.

I. The Genus *Albugo*. *Bull. Tor. Bot. Club.* **34**: 61, 1907.

II. *Phytophoreæ* and *Rhysothecææ*. *Ibid.* **34**: 387, 1907.

III. New or Noteworthy species (Species of *Albugo* and *Peronospora*, *Ibid.* **35**: 361, 1908.

IV. Host Index. *Ibid.* **35**: 543, 1908.

During this process the nuclei enlarge, undergo one or two mitoses, Fig. 64, and in some species all the nuclei except one pass to the periplasm. In other species the oosphere is multinucleate at

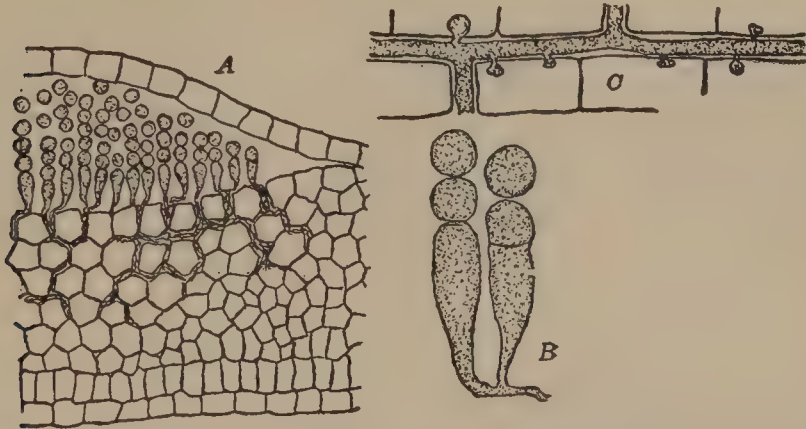


FIG. 60.—*Albugo*. A, section through a sorus showing epidermis, conidia, conidiophores and mycelium; B, conidiophores and conidia; C, mycelium and haustoria. After Bergen and Davis.

maturity, Fig. 61. The latter type is fertilized by numerous nuclei from the antheridium, the former by a single nucleus. After fertilization the oosphere matures to form an oospore.

The globular oöspores fall into two classes; first tuberculate or ridged; second, reticulated. These are illustrated in Fig. 62.

While the conidial stages are common, oöspores are less so. Conidia germinate freely only if they are chilled, and in germination usually produce several ovate zoöspores with unequal, lateral cilia. After a brief period of motility they became walled and produce germ tubes capable of infecting susceptible hosts. The oöspores after a period of rest germinate in a similar manner.

Albugo is readily recognized from its conidial sori and the species can usually be inferred by means of a host index; though for accurate determinations oöspores are needed.

A. candida (Pers.) Roussel. Sori on all parts of the host except the roots, white or rarely light yellow, prominent and rather deep-



FIG. 61.—Multiple fertilization in *A. bliti*. Antheridial tube discharging sperms. After Stevens.

seated, variable in size and shape, often confluent and frequently producing marked distortion of the host; conidiophores hyaline, clavate, about $35-40 \times 15-17 \mu$; conidia, globular, hyaline, with

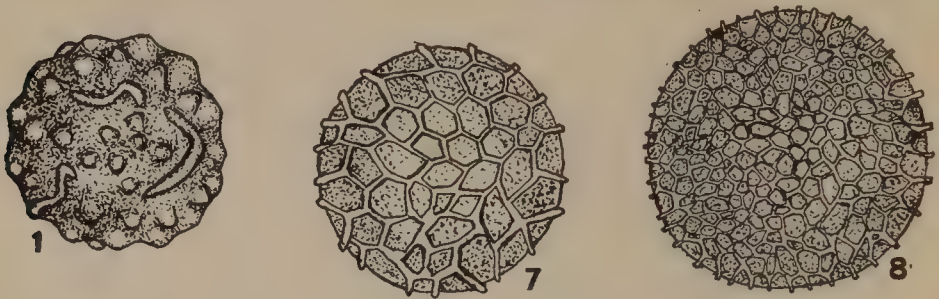


FIG. 62.—Oöspores of *Albugo*. 1. *A. candida*. 7 *A. bliti*. 8. *A. platensis*. After Wilson.

uniformly thin walls, $15-18 \mu$; oöspores, much less common than conidia, usually confined to stems and fruits, chocolate-colored, $40-55 \mu$; epispore thick, verrucose, or with low blunt ridges which are often confluent and irregularly branched.

This is the most widely distributed and most common species of the genus. It occurs throughout the world on a large number

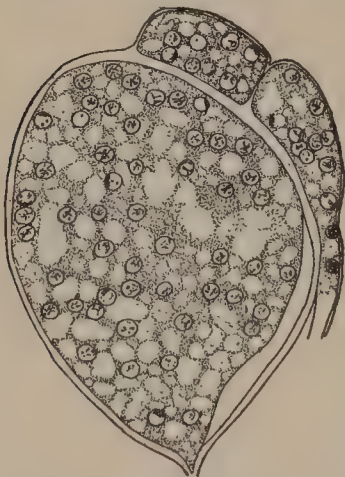


FIG. 63.—*A. bliti*, young oögonium and antheridium showing nuclei. After Stevens.



FIG. 64.—*A. bliti*, showing differentiation of cytoplasm and periplasm, the nuclei in mitosis. After Stevens.



FIG. 65.—*A. bliti*, antheridium showing the multinucleate tube. After Stevens.

of cruciferous hosts, and often gives rise to very pronounced hypertrophy. Practically all cultivated crucifers, cabbage, radish, turnip, horseradish, etc., are subject to attacks of this fungus, as also are the caper, mignonette, and *Tropæolum*.

A. ipomœæ-panduranæ (Schw.) Sw. Sori amphigenous or caulicolous, white or light yellow, prominent, superficial, 0.5–20 mm., rounded, often confluent and frequently producing marked distortions of the host; conidiophores hyaline, clavate, unequally curved at base, $15 \times 30 \mu$; conidia hyaline, short-cylindric, all alike or the terminal more rounded, $14\text{--}20 \times 12\text{--}18 \mu$; the membrane with an equatorial thickening, usually very pronounced. Oösporic sori separate from the conidial, caulicolous, $1\text{--}2 \times 5\text{--}6$ cm. or even more, causing marked distortion; oöspores light yellowish-brown, $25\text{--}55 \mu$; epispore papillate or with irregular curved ridges.

Common throughout the world on various species of Convolvulaceæ; morning glory, moon flower, sweet potato, etc., although causing but little damage.

A. tragopogonis (DC.) S. F. Gray. Sori hypophyllous or caulicolous, prominent, deep-seated, white or yellowish, pulverulent, rounded or elongate, $1\text{--}3 \times 1\text{--}8$ mm; conidiophores hyaline, clavate, about $12\text{--}15 \times 40\text{--}50 \mu$; conidia, $12\text{--}15 \times 18\text{--}22 \mu$; light yellow or hyaline, short-cylindric, the terminal larger and less angular than the others, membrane with an equatorial thickening; oöspores produced in stems and leaves, dark brown or almost black at maturity, opaque, $44\text{--}68 \mu$, epispore reticulate, areolæ 2μ ; wing bearing papillate tubercles at its angles.

A cosmopolitan species on the Compositæ. Salsify is the chief economic host.

A. occidentalis Wils. is reported on the beet; **A. portulacæ** (DC.) Kze. on purslane and **A. bliti** (Biv.) Kze. on Amaranthus, beet and related plants.

Peronosporaceæ¹ (p. 63)

The members of this family produce the diseases commonly known as the "downy mildews." They contain many important plant pathogens. The oöspores are in general indistinguishable from those of *Albugo* but the conidiophores are quite different, being aerial instead of subepidermal. In most cases they are branching and tree-like, Fig. 69, but in a few genera they are short. The oospore in *Peronospora* and *Sclerospora* is formed as in *Albugo* resulting when mature in an uninucleate egg surrounded by a

¹ Farlow, W. G. Enumeration of the Peronosporaceæ of the U. S. Bot. Gaz. 8; 305, 1883.

periplasm bearing the degenerate supernumerary nuclei. Fertilization is as in the *Albugos* that have an uninucleate egg.

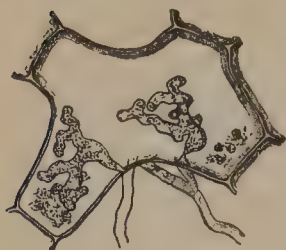


FIG. 66.—Haustoria of a *Peronospora*. After Zopf.

The family has suffered many revisions of classification and much renaming of genera. *Plasmopara* and *Peronospora* are especially rich in a masquerade of names.

In practice *Sclerospora* is readily recognized by its oöspores; *Bremia* by the peculiar formation of the apices of the conidiophores (Fig. 71). The remaining genera Nos. 2, 3, 5 are closely related and difficult of differentiation. In addition to the key characters, the general habit of the conidiophores as shown in Figs. 69, 72 aids in distinguishing *Plasmopara* from *Peronospora*, while *Pseudoperonospora* is intermediate between these two in mode of branching.

KEY TO GENERA OF *Peronosporaceæ*

- Conidiophores regularly monopodially branched; with the main axis not indurate, conidia germinating by zoöspores or by a plasma
 - Conidiophores fugacious, stout, sparingly branched; oöspore permanently united to the wall of the oögonium. 1. *Sclerospora*, p. 75.
 - Conidiophores persistent, slender, usually freely branched; oöspore free from the wall of the oögonium
 - Branches of the conidiophore apically obtuse. 2. *Plasmopara*, p. 76.
 - Branches of the conidiophore apically acute. 3. *Pseudoperonospora*, p. 78.
- Conidiophores dichotomously branched; conidia germinating by a germ tube.
 - Conidiophores with subapical disk-like enlargements from which the ultimate branchlets arise radially; germ tube produced from the apex of the conidia. 4. *Bremia*, p. 79.
 - Conidiophores without subapical enlargements; conidia germinating from the side. 5. *Peronospora*, p. 80.

Sclerospora Schröter (p. 74)

This genus differs from all other Peronosporales in the preponderance of its oöspores; these are the conspicuous stage, while the conidiophores and conidia are few, small and evanescent. An exception to this statement apparently occurs in *S. philippinensis*.

Mycelium much branched, with small vesicular haustoria; conidiophores erect, solitary or in groups of two or three, fugaceous, low and stocky, sparsely branched, the branches also stocky; conidia elliptic or globose-elliptic, hyaline, smooth; oöspores globose, intramycelial, the episore brown, irregularly wrinkled, permanently united to the persistent wall of oögonium.

S. graminicola (Sacc.) Schr. infects leaves and inflorescences, the oöspores causing marked distortion of the latter and rapid



FIG. 67.—*S. graminicola*. Conidiophores and conidia; germinating conidia and zoöspores. After Butler.

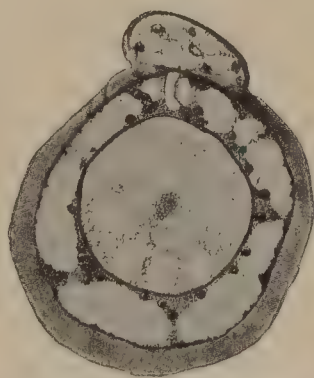


FIG. 68.—*S. graminicola*, oögonium, oöspore and antheridium in section. After Stevens.

disintegration of the former; conidiophores $100 \times 10-12 \mu$, conidia $20 \times 15-18 \mu$; oögonium wall thick, $4-12 \mu$, at maturity $30-60 \mu$ in diameter, reddish-brown; oöspore pale brown, $26-36 \mu$.

The conidial phase is not prominent, while the oöspores by their disintegrating effect upon the leaves of the host, render the plants quite conspicuous and closely simulate the habit of a brown smut. On millet (*Setaria italica*), pearl millet, fox tail and corn.

S. macrospora Sacc. has been reported in corn tassels and on wheat. Conidia unknown; oögonia embedded firmly in the tissue

of the host, not causing disintegration as in *S. graminicola*; oöspores light yellow, smooth, 60–65 μ .

S. philippinensis Weston¹ causes serious disease of corn in the Philippines. Conidia common and abundant; oöspores rare, not seen on corn. Conidiophores emerge from the stomata, 150–400 μ long x 15–26 μ thick, dichotomously branched 2–4 times. Conidia 27–39 x 17–21 μ .

S. spontanea Weston, a closely related species, occurs on sugarcane, sorghum and corn.

Plasmopara Schröter (p. 74)

The tree-like, branching conidiophores, Fig. 69, are common to this genus, *Peronospora*, *Pseudoperonospora* and *Bremia*, and unlike the conidiophores of *Phytophthora* they are completely formed before they begin to bear spores.

Mycelium branched; haustoria simple; conidiophores erect, solitary or fasciculate, from the stomata of the host, monopodially branched, the branches arising at right angles to the main axis, as do also the secondary branches (at least never appearing truly dichotomous) the ultimate branches apically obtuse; conidia globose to ovoid, hyaline or smoky, germinating by zoöspores or the entire protoplasmic mass escaping and then sending out a germ tube; oöspore globose, yellowish-brown, the epispore variously wrinkled sometimes appearing somewhat reticulate; oogonium persistent, but free from the oöspore.

P. viticola (B. & C.) B. & d T., collected in 1834 by Schweinitz and regarded as a *Botrytis* was first published in 1851.

Hypophyllous, caulicolous, or on young fruits, covering the infected areas with a white, downy growth; on the leaves epiphyllous discoloration yellowish; on the fruit often causing a brown rot without producing conidia; conidiophores fasciculate, 250–850 x 5–8 μ , 4–5 times branched, the ultimate branchlets about 8 μ long; conidia ovate-elliptic, very variable in size, 9–12 x 12–30 μ ; oöspores 30–35 μ , epispore brown, wrinkled, or almost smooth; oogonium thin-walled, hyaline or light yellowish-brown.

The mycelium on *Vitis* is found in all diseased tissues except the xylem. The conidiophores issue from stomata. The conidia germinate readily in water, producing in about three-fourths of an hour biciliate zoöspores. These after fifteen to twenty minutes activity

¹ Weston, Wm. H. Philippine downy mildew of maize. Jour. Agr. Res. 19: 97, 1920.

cease motion, round off, become walled, then germinate by a tube. This tube bores through the epidermis and develops into the internal mycelium. Infection is almost exclusively from the lower side of the leaf, and through the stomata, and is followed by typical spots in about 11 days. Oöspores are much more rare than co-

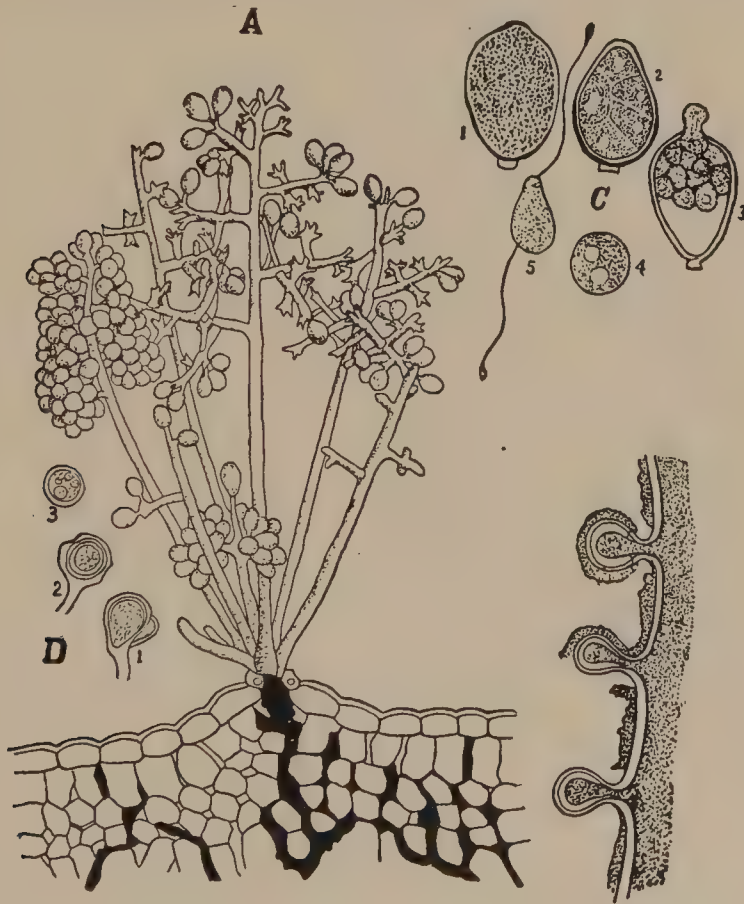


FIG. 69.—*P. viticola*. A, section of a leaf with conidiophores emerging from a stoma; C, formation of swarm-spores; D, formation of oöspores. After Millardet.

nidia but are often found in autumn, sometimes two hundred to a square millimeter of leaf surface. Though hibernation is doubtless chiefly by oöspores it has been shown that the mycelium can perennate in old wood, and even form oöspores therein. The fungus is dependent on abundant moisture.

Other species are on umbellifers including the parsnip and carrot, currant, *Helianthus*, *Impatiens*, *Aconitum* and cultivated hepaticas.

Pseudoperonospora Rostew. (p. 74)

There are four species which have been variously designated as *Peronospora*, *Plasmopara*, *Pseudoperonospora* and *Peronoplasmodium*. The genus combines colored conidia and zoösporic germination with a type of conidiophore intermediate between those of *Peronospora* and *Plasmopara*.

Mycelium much branched; haustoria small, usually simple; conidiophores pseudo-monopodially branched, the ultimate branchlets acute, the primary arising at acute angles; conidia colored, elliptic, conspicuously papillate both apically and basally; oöspores thin-walled, smooth or roughened; oogonium thin-walled.

P. cubensis (B. & C.), Rostew.

Hypophyllous, rarely amphigenous; discoloration of the host yellowish or water-soaked; conidiophores 1-2 rarely more from a stoma, 180-400 x 5-9 μ , 3-4, rarely 2-5 times branched, the ultimate branchlets recurved; apically acute, 5-20 μ long; conidia gray, brownish or smoky, ovoid to ellipsoid, papillate, 20-40 x 14-25 μ ; oöspores spherical, yellowish, warty-papillate, 30-43 μ , maturing in the decaying leaves.

The intercellular hyaline, irregular, branching mycelial threads abound in the spongy parenchyma, penetrating the cells by short, ovate haustoria. The conidiophores emerge through stomata, or rarely directly through the cuticle, near the invasion line of the fungus. Fresh conidia germinate in water in two to four hours forming flattish zoöspores with one anterior and one posterior cilium. The zoöspores later become spherical, walled and develop a germ tube. These germ tubes enter the host through the stomata or directly through the cuticle from either above or below. Moist weather is favorable to the fungus in that conidia are produced more abundantly and retain their power of germination longer when moist. Disease spots appear two or three days after infection; conidia some nine or ten days after infection. When the invaded host cells die the conidiophores therefrom cease to function.

For many years after its discovery in 1868 in Cuba this fungus was not well known even scientifically, its first serious outbreak being about 1889. It appeared in Japan about the same time and is now known to be almost cosmopolitan. Oöspores have not been seen in America. Many wild and cultivated cucurbits are infected, among them the pumpkin, squash, cucumber, muskmelon, watermelon, and gourd. The fungus is especially prevalent on cucum-

bers raised under glass. Clinton infected muskmelons with spores produced on cucumber.

P. celtidis (Waite) Wil. on hackberry and *P. portoricensis* Lam.



FIG. 70.—*P. cubensis*: 3. Conidiophore with young and old conidia. 5. Conidium. 6. Conidium germinating. 11. Zoospores. 18. Infection through a stoma. After Clinton.

on the chinaberry are the only species in the family that infect dicotyledonous trees.

P. humuli Miy. & Taka causes hop disease.

Bremia Regel (p. 74)

This genus resembles *Peronospora* except that just below the ends of the conidiophore branches there are pronounced swellings from which spring radially a number of short branches each bearing an ovate, papillate conidium. The conidia germinate by apical germ tubes. There is only one species.

B. lactucæ Regel is found on lettuce and several other of the Compositæ.

Hypophyllous or amphigenous, causing discoloration, then wilting of the host; conidiophores produced singly but in great abundance, much branched; conidia ovate, $16\text{--}22 \times 15\text{--}20 \mu$; oöspores small, $26\text{--}35 \mu$, light brown, the epispore wrinkled.



FIG. 71.—*B. lactucæ*.
After Tubeuf.

Peronospora Corda (p. 74)

This genus contains several aggressive parasites. Its conidiophores are much like those of *Plasmopara* but with more tendency to dichotomous branching and to more graceful habit; the apices are acute.

Mycelium well developed, haustoria filiform, simple or branched; conidiophores dichotomously 2–10 times branched at acute angles, ultimate branchlets acute, more or less reflexed; conidia hyaline or colored, papillate, germinating directly by lateral germ tubes; oöspores globose, reticulate, tuberculate, wrinkled or smooth.

P. parasitica (Pers.) de Bary. This is often associated with *Albugo candida*, giving it the appearance of a parasite on that fungus. Almost all species of Cruciferæ are subject to attack, among them cabbage, cauliflower, radish, collards, turnips, horseradish, and others of minor economic importance. It is cosmopolitan in distribution.

The fungus covers any green part of the host with a dense, white growth, often causing hypertrophy, especially in oöspore formation; conidiophores $200\text{--}300 \times 10\text{--}12 \mu$, bushy branched, stout, deliquescent, with 5–8 main branches, each from 3–7 times branched, ultimate branchlets slender, more or less curved, usually arising at acute angles, about $12\text{--}15 \times 2\text{--}3 \mu$; conidia broadly elliptic, blunt, often becoming globose, about $12\text{--}22 \times 24\text{--}27 \mu$, hyaline or very light; oöspore globose, yellow-brown, $26\text{--}45 \mu$, epispore smooth or wrinkled; oogonium thick, colorless.

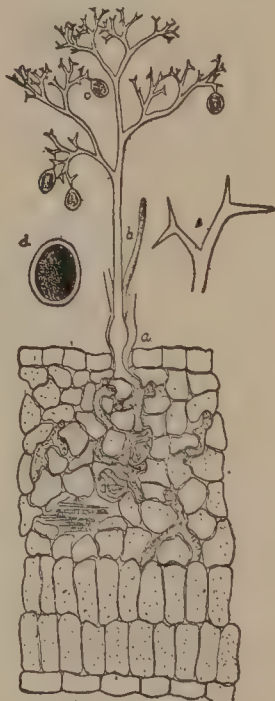


FIG. 72.—*P. effusa* on spinach. After Halsted.

P. effusa (Grev.) Rab. causes a serious disease of spinach. It also occurs on a wide range of weeds of the Chenopodiaceæ.

Hypophyllous, causing yellow or brown discolorations, the mass of conidiophores of a violet cast; conidiophores $150-400 \times 7-9 \mu$, much branched, the ultimate branches at right angles, usually recurved, $8-15 \times 3-4 \mu$; conidia ellipsoid to globose $17-18 \times 22-24 \mu$, violet or smoky; oöspores globose, $30-40 \mu$, epispore light brown, more or less regularly wrinkled; oögonium thin, brown.

P. schleideni Ung. was first described as a Botrytis in 1841. It was noted in America in 1872.

The conidia in mass present a purplish tint. The conidiophores usually emerge singly through the stomata. The mycelium is intercellular and from it slender, branched haustoria are given off to the parasitized cells, their ends often wrapped around the nuclei. In water the conidia germinate directly to form an infective tube (Fig. 73) which enters the host through the stomata. Conidia retain their germinating power only a few hours. Fertilization occurs much as in *P. parasitica* (Fig. 73) and the sexual spores, which abound, serve for hibernation. They may live several years.

The fungus is found on onion, garlic, etc. (*Allium* sps.), covering leaves with a dense growth; conidiophores, 3-6 times branched, $300-700 \times 12-15 \mu$; branches 2-5, scattered, ultimate branchlets subulate, $15-20 \mu$, more or less recurved; conidia large, obovate to pyriform, basally papillate, $45-58 \times 20-25 \mu$, the membrane violet; oöspore globose, light-brown, about 30μ , epispore smooth or slightly wrinkled.

P. trifoliorum de Bary. Hypophyllous, forming a dense, grayish or dirty-white growth over the host; conidiophores slender, $360-600 \times 9-11 \mu$, 6-8 times branched at acute angles, the primary branches rather erect, the secondary more spreading, flexuose, more or less recurved, ultimate branchlets at right or obtuse angles, straight, subulate, $7-12 \times 7-3 \mu$; conidia globose to broadly elliptic, $15-20 \times 18-36 \mu$, violet; oöspores globose, $24-30 \mu$, epispore light brown, smooth.

It causes serious loss to clover and species of related genera, particularly alfalfa.

It differs from *P. viciæ* in the branching of the conidiophores, the lighter color of the spot and fungus, and the smooth oöspores.

P. viciæ Berk. Hypophyllous or caulicolous, covering the host with a grayish-violet growth, epiphyllous discolorations yellowish

or inconspicuous; conidiophores fasciculate, $300-700 \times 9-11 \mu$, 5-8 times branched, the main branches arising at acute angles,

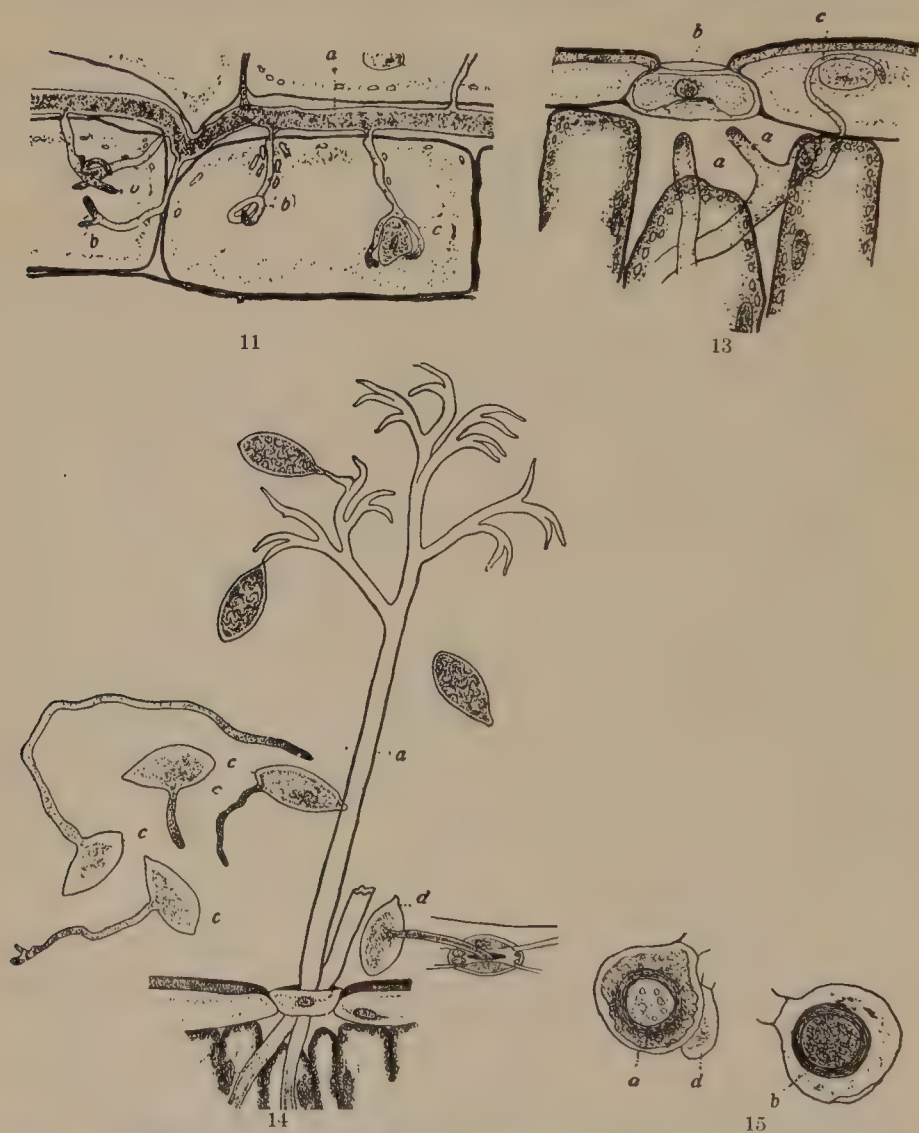


FIG. 73.—*P. schleideni*. 11. Mycelial threads between the large conductive cells of the leaf; (a) the mycelial thread; (b, b) branched or coiled haustoria; (c) branched haustorium wrapped about the nucleus. 13. Young conidiophores, (a, a) turning toward the stoma, (b); (c) haustorium wrapped about the nucleus of the epidermal cell. 14. Mature conidiophore (a) with mature conidia, (c, c.); (d) germ tube of conidium entering stoma. 15. Oöspores, (a) mature oöspore with old antheridium, (d) still attached; (b) mature oöspore still inclosed in the old wall of the oögonium. After Whetzel.

erect, the ultimate subequal, slightly flexuose, arising at right or obtuse angles, the lateral recurved, $10-17 \times 2-3 \mu$; conidia elliptic.

P. hyoscyami de Bary appeared on tobacco in Florida in 1921 in apparently serious form.

Other species are on *Rubus*, strawberry, rose, violet, pansy, *Colocasia*, primrose, forget-me-nots and many other plants.

Zygomycetes (p. 56)

This group of fungi is readily distinguished from the Oömycetes by its isogamous sexual organs, when these are present. In the

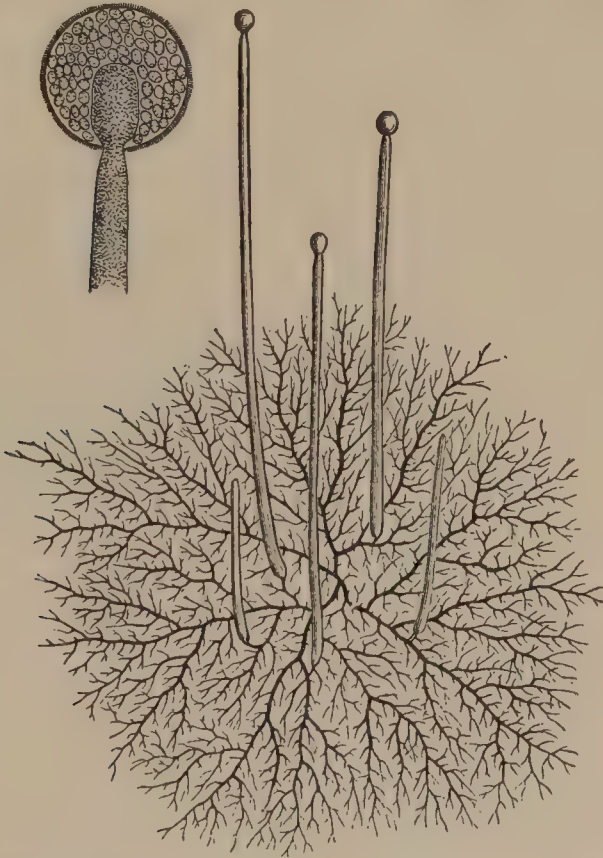


Fig. 74.—A sporangium with a columella (*Mucor*). After Sachs.

absence of sexual organs the general type of sporangium is usually sufficient mark of distinction for those who are even but slightly acquainted with the two groups. The mycelium, if young, serves to indicate relationship to the Phycomycetes. Older mycelium is often septate and would lead the unwary into errors of classification.

Asexual spores are either in sporangia or are borne as conidia. The spore-bearing stalks exhibit wide diversity in shape and form of branching.

Sexual spores (**zygotes**) are produced through the union of two like gametangia. (Fig. 75).

Mucorales¹ (p. 56)

This order is comprised mainly of saprophytes; but includes a few forms which prey upon vegetation in a very low ebb of life, as cells of ripe fruit, tubers, etc., and a few species which are of especial interest as they grow upon other fungi. The sporangial

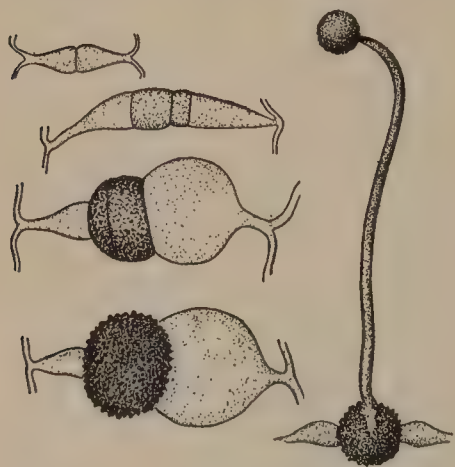


Fig. 75.—*Mucor*: zygospore formation. After Brefeld.

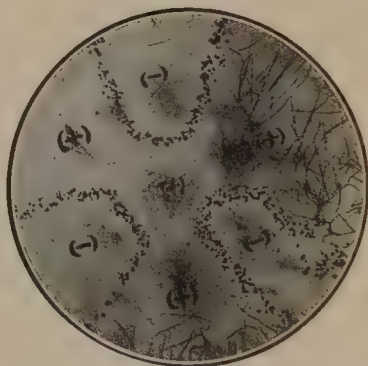


Fig. 76.—*Phycomycetes* showing zygosporic lines at regions of contact between + and - strains. After Blakeslee.

stage is exceedingly common; the zygosporic much less so, very rare in the case of some species. Blakeslee has shown that in some species, though the two uniting sexual organs are to all appearances alike, the plants are in reality dioecious; that a branch from one plant cannot produce sexual organs that will unite with other sexual organs produced upon the same plant. Moreover, there appears to be a differentiation of sex in that one plant, which may provisionally be regarded as the male, unites freely with another plant, provisionally the female, but this male plant refuses to unite with any other plant which is capable of uniting with the female and all plants that can unite with the male refuse to unite

¹ Sumstine, D. R. The North American Mucorales. I. *Mycol.* **2**: 125, 1910.

with the females. In some species the plants of one sex show a more luxuriant vegetative growth than do plants of the other sex.

KEY TO FAMILIES OF **Mucorales**

- Asexual spores in typical sporangia, although in some genera few spored; sporangium with columella; zygospores naked or thinly covered with outgrowths of the suspensor.....**Mucoraceæ**, p. 85.
 Asexual sporangia of two kinds, polysporic and monosporic.....**Choanephoraceæ**, p. 86.

Mucoraceæ

Asexual spores in typical sporangia, although in some genera few-spored; sporangium with columella; zygospores naked or thinly covered with outgrowths of the suspensor.

Mycelial threads all alike or of two kinds, one aërial, the other buried in the substratum, coenocytic during growth but septate at maturity; reproduction by asexual spores borne in sporangia and by zygospores formed by the union of equal gametes; sporangiophores simple or branched; sporangia variable, typically with a columella and many spores, but in some genera some of the sporangia are few-spored and without columellas; zygospores variable, smooth or spiny, borne on short branches of the mycelium.

Rhizopus Ehrenberg ¹

Sporangial membrane thin and fugaceous throughout; sporangia all similar; mycelium differentiated into a colorless vegetative and a colored aërial region. Aërial mycelium stoloniferous, zygospores formed in the substratum; sporangiophores arising from the nodes.

The sporangium wall is not cutinized and falls away. The sporangia are all of one kind with columellas. The sporangiophore is never dichotomous. The suspensor is without outgrowths.

R. nigricans Ehr. Aërial mycelium at maturity chocolate colored; rhizoids numerous; sporangiophores fasciculate, erect, aseptate; sporangia globose, blackish-olive, granular; columella hemispheric; spores gray to brown, subglobose or irregular, 11–14 μ ; zygospore 150–200 μ , epispore with rounded warts, black. This

¹ Hanzawa, J. Studien über einige *Rhizopus*-Arten. *Myc. Cent.* **5**: 231, 1915.

is the cause of soft rot of stored vegetables and fruits, particularly of sweet potatoes, Irish potatoes, beans, apples, pears, tomatoes, strawberries, peaches, plums, raspberries, currants and quince. It also causes death of squash blossoms and is destructive to barley



Fig. 77.—*Rhizopus*. Diagram showing mycelium and sporangiophores. After Coulter, Barnes and Cowles.

during malting. It is distinctly a wound parasite and is unable to force entrance through a sound epidermis.

On strawberries the mycelium passes between the cells, along the middle lamellæ, and causes the protoplasm of adjacent cells to shrink. A temperature of 8°C. decidedly retards its growth, but its

rate of growth increases rapidly with rise of temperature above that point.

The richly branched mycelium which varies from very thin and hyaline to thick, coarse and slightly fuscous, is found throughout the rotten portion of the hosts. After a period of luxuriant vegetative growth hyphæ protrude to the air, first through existing ruptures in the epidermis, later by rifts forced by the fungus itself. Sporangiophores then form in dense bush-like growths, each bearing one terminal sporangium. The sporangia are at first white, later black and contain very numerous spores. Aërial stolon-like hyphæ reach out in various directions and at their points of contact with some solid develop holdfasts (Fig. 77) and a new cluster of sporangiophores.

Zygotes are produced by union of two mycelial tips as is shown in Fig. 75.

Rhizopus tritici Saito,¹ which causes a similar rot of sweet potatoes, has been extensively studied regarding its production of amylase. Six other species have by inoculation experiments been shown capable of rotting sweet potatoes.

Choanephoraceæ (p. 85)

Mycelium parasitic on living plants; sporangia of two kinds; macrosporangia globose, columella small, spiny, spores few, on

¹ Harter, L. L. Amylase of *Rhizopus tritici* with a consideration of its secretion and action. Jour. Agr. Res. **20**: 761, 1921.

simple or branched, erect sporangiophores; microsporangia clavate, one-spored simulating conidia and borne in heads on the enlarged apices of umbellately branched sporangiophores; zygospores as in *Mucoraceæ*.

Choanephora cucurbitarum (B. & Rav.) Thaxt.¹ is the cause of decay of cucurbits, especially pumpkins, also of okra. It also blights the blossoms.

ASCOMYCETES (p. 55)

The distinguishing mark of this group is the **ascus**. This in its typical form is shown in Fig. 78, as a long, slender or club-shaped sac in which the spores are borne. The number of spores in the ascus is usually definite and is commonly of the series, 1, 2, 4, 8, 16, 32, 64, etc., the most common number being 8. The spores vary in size, color, shape, markings, and septation. The asci in most genera are arranged in a definite group, a layer, constituting the **hymenium** which may be either concave, convex, or flat. Between the asci in the hymenium are often found slender hyphal threads of various form, the **paraphyses**, Fig. 78.

The hymenium may be borne in or upon a firm substratum of woven threads, the **stroma**, or upon a very tenuous substratum, the **subiculum**, or without any definite subascal structure. The stromata vary widely in character, size, texture, color, surface, form, etc.

The mycelium is usually abundant, branched and septate, the septation readily distinguishing this group from the *Phycomycetes*. In many species the mycelium weaves together into a false parenchyma and constitutes relatively large spore-bearing structures. Fig. 79.

The ascigerous organ, **ascocarp**, or **ascoma**, if saucer-shaped and open is an **apothecium**, Fig. 109, if closed a **perithecium**, Fig. 159. In other cases, the ascigerous layer covers the exterior surface. Fig. 79.

On the boundary lines between the *Ascomycetes* and other groups are fungi which do not present the typical *Ascomycete*



FIG. 78.—Portion of a hymenium showing asci and paraphyses. After Chamberlain.

¹ Wolf, F. A. A squash disease caused by *Choanephora cucurbitarum*. Jour. Agr. Res. 8: 319, 1917.

picture but which are regarded as probably belonging to the group, i, e., transition forms between this and other groups. Among such are forms in which the asci are without either stroma or covering (Protodiscales, p. 95); others in which the asci are not even in groups but are scattered irregularly throughout the ascocarp

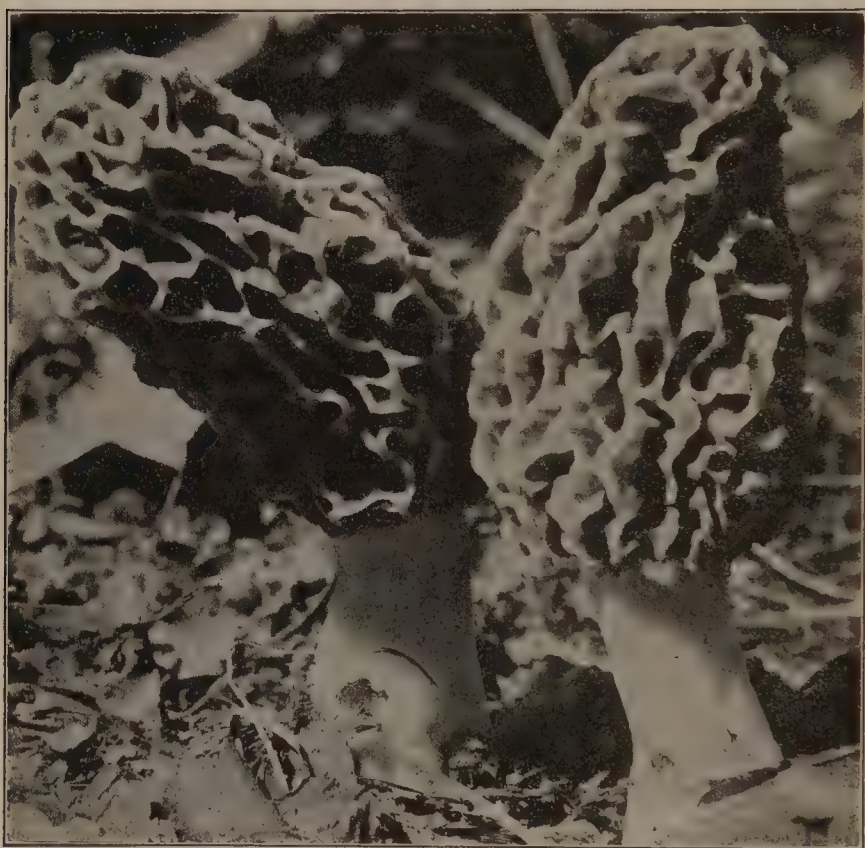


FIG. 79.—The large ascocarp of the morel. After Freeman.

(Aspergillales, p. 122); and still others with the asci neither in regular groups nor covered (Protoascomycetes, p. 92).

Besides the ascus the Ascomycetes possess many other kinds of reproductive structures in the form of conidia. These may be borne singly or in rows on simple or branched conidiophores.

The conidiophores may be single or variously grouped in columns or layers. Figs. 377, 391, 393. In some instances they are very short, innate; again they are long, loose or floccose. They may emerge through stomata singly or in tufts or they may form sporog-

enous cushions below the epidermis, or again they may be borne inside of a hollow structure, the **pycnidium**, which covers them. **Chlamydospores** are also found. One or several distinct types of sporification may belong to one species of Ascomycete. These different forms of spores may appear simultaneously on the same mycelium or they may follow in definite succession regulated by the changes in environment, or again one or more of the spore forms belonging to the life history of the fungus may be omitted for long intervals to appear as the result of stimuli of which little is yet known.

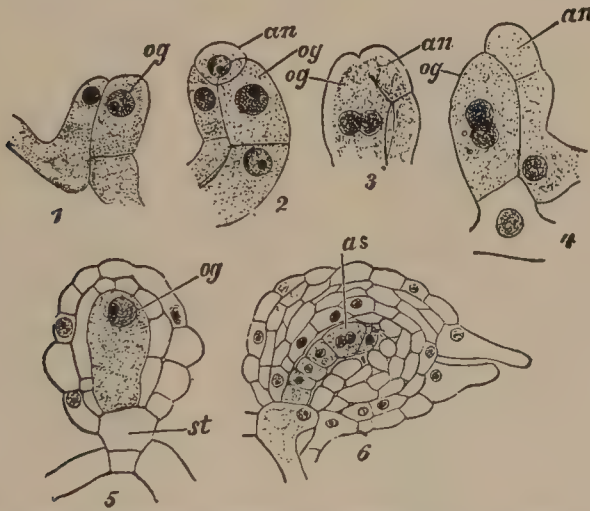


FIG. 80.—*Sphærotheca castagnei*. Fertilization and development of the perithecium. Og = oogonium, an = antheridium, st = stalk-cell. 6 as = the ascogonium derived from the oogonium. After Harper.

Frequently the conidial stage prevails as a vigorous destructive parasite throughout the growing season while the ascigerous stage appears only during winter or after hibernation, developing only on dead tissue and as a saprophyte.

The conidia and chlamydospores are asexual spores. Sexuality in the great majority of Ascomycetes has not been investigated, but in some species fertilization is known to occur. In many species, at least in form similar to that shown by the Phycomycetes, it is absent, probably having been lost by degeneration or else very much modified.

In some of the Discomycetes there is one or more carpogonia and fertilization occurs through a trichogyne by spermatia; a mode often met among the lichens.

In *Pyronema*, Fig. 83, the carpogonium is multi-nucleate and it is fertilized by a multi-nucleate antheridium through a trichogyne.

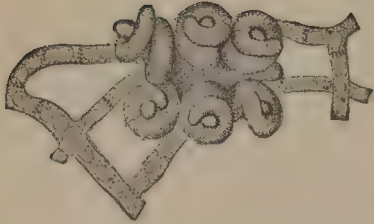


FIG. 81.—*Boudiera*. Six sets of sexual organs. After Claussen.



FIG. 82.—Later stage than that of Fig. 81 showing asci and ascophores. After Claussen.

Fusion of nuclei is probably in pairs as in *Albugo bliti* of the Phycomyces. In *Boudiera* a similar relation is found. Figs. 81, 82.

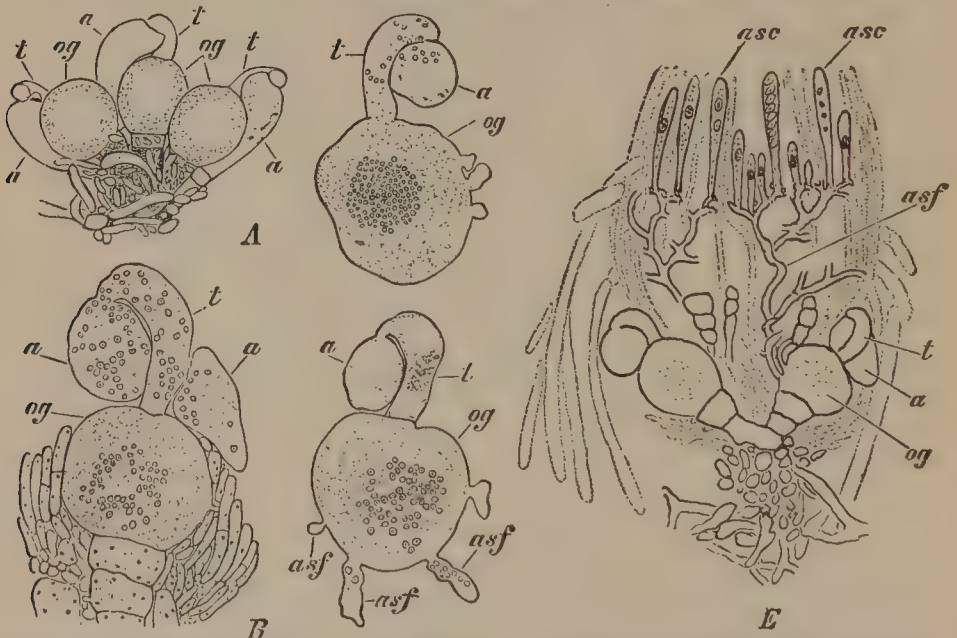


FIG. 83.—*Pyronema confluens*. A. the sex organs, og = oögonium, t = trichogyne. B. fertilization stage, C. section through young apothecium, asc = asci, asf = ascogenous filament. After Harper.

In some *Perisporiales* an uninucleate oögonium is fertilized by an uninucleate antheridium. Fig. 80.

The oögonium after fertilization gives rise to a more or less complicated system of **ascogenous hyphæ**, very simple in the Erysiphaceæ, very complex in some Discomycetes, which produces the asci. The sterile parts of the ascocarp, the paraphyses and enveloping structures, arise from parts below the oögonium and antheridium.

The very young ascus usually receives two nuclei from the parent strand of the ascogenous hypha. These nuclei unite giving the primary-ascus-nucleus. This by successive mitoses affords the single spore-nuclei. The spores are cut out from the protoplasm



FIG. 84.—Tip of ascus of *Erysiphe* showing delimitation of ascospore from ascoplasm by astral rays. After Harper.



FIG. 85.—Later stage than Fig. 84, showing well defined spore-wall. After Harper.

of the ascus in a most peculiar manner by reflexion of, and union of, astral rays which emanate from a centrosome-like organ at the beak of the prolonged nucleus. Figs. 84, 85.

The significance of two nuclear fusions in the life cycle of these fungi, one following the union of the antheridium with the oögonium, the other later, in the asci, is a puzzling phenomenon, the real meaning of which is not clear.

KEY TO SUBCLASSES OF **Ascomycetes**

Asci with definite number of spores

Asci separate or scattered 1. **Protoascomycetes**, p. 92.

Asci approximate, usually forming a

hymenium 2. **Euascomycetes**, p. 94.

Subclass **Protoascomycetes** (p. 91)

There is a single order, the Saccharomycetales,¹ with about seventy species.

Mycelium often undeveloped; asci isolated or formed at different points on the mycelium, mainly 4-spored; spores unicellular; asexual reproduction by gemmation or by conidia.

KEY TO FAMILIES OF **Saccharomycetales**

- Vegetative cells single or loosely attached in irregular colonies, mycelium not usually developed, asci isolated, not differentiated from vegetative cells. . . 1. **Saccharomycetaceæ**, p. 92.
- Vegetative cells forming a mycelium, asci terminal or intercalary, differentiated from mycelium. 2. **Endomycetaceæ**, p. 93.



FIG. 86.—Yeast plant-bodies, showing budding and sporulation. After Coulter and Rees.

The first family, the yeasts, to which belong the majority of the species of the order, is of prime importance in fermentation. A few species are known to cause animal diseases; others are found associated with the slime fluxes.

Saccharomycetaceæ¹

Vegetative cells separate or few together, never truly filamentous, propagating by buds; asci globose to elliptic, 1–4, rarely 8 to 12-spored; growing typically in sugary or starchy materials.

Nematospora Peglion

Colonies (in culture) disciform; cells elongate; asci cylindric, 8-spored; spores filiform, continuous, long-ciliate, hyaline.

N. coryli Pegl., the cause of malformation of the hazel nut is a peculiar fungus with what appears to be asci containing eight, long, slender, flagellated spores.

¹ Guillermond, A. The Yeasts. Trans. by F. W. Tanner. John Wiley and Sons, London, 1920.

N. phaseoli Wingard ¹

Elliptical cells in young cultures vary in length from 8–14 μ and in diameter from 6–10 μ . The mature spherical cells are 20 μ in diameter and the mycelium-like strands from 90–140 x 2.5–3.5 μ . Asci and ascospores are produced in great numbers in the lesions on Lima bean seed. They are cylindrical with rounded ends, 60–85 x 10–12 μ ; ascospores, 8, in two groups of 4, 40–46 x 2.5–3 μ , slender, 1-septate, slightly ridged at septum, apex acute, base extended into a slender, non-motile whip which averages about one and one-fourth times the spore length.

Endomycetaceæ (p. 92)

Mycelium usually well developed, often producing a luxuriant growth, multiseptate; asci borne singly on branches or intercalary, 4 to 8-spored; spores one-celled; conidia produced apically, unicellular.

Endomyces Rees

Mycelium well developed, byssoid; asci asexually produced, borne singly on the ends of short lateral branches, globose to pyriform, 4-spored; spores continuous.

The members of this genus are of questionable importance as parasites. Some are commonly found in sap exuding from tree wounds where they, together with other fungi present, set up a fermentation the products of which prevent the wound from



FIG. 87.—Young asci of *E. mali*, spores later form in these. After Lewis.



FIG. 88.—*E. mali*. Typical manner of bearing conidia on agar. After Lewis.

healing and result in injury. One species has been reported in America as an active parasite on apples.

E mali Lewis

Mycelium well developed, multiseptate; conidia formed on short conidiophores or on the ends of short germ tubes, averaging 3 x 8 μ ; no yeast-like budding; asci usually on short lateral branches, 11–14 μ in diameter; ascospores sphaeroidal, slightly elongate, 4.5 x 5.5 μ with thickened places on the walls, brown when mature. Figs. 87, 88.

¹ Wingard, S. A. Yeast-Spot of lima beans. *Phytoph.* **12**: 525, 1922.

Euascomycetes (p. 91)

This is an extraordinarily large group comprising some 16,000 species, with great variety of size, color and shape of plant body. Most of them are saprophytes, still many are parasites either in their ascigerous or their conidial stages of development.

The twelve orders of chief interest as plant parasites are given in the following key.

KEY TO ORDERS OF Euascomycetes

- Asci approximate in an indefinite hymenium, no ascoma. 1. **Protodiscales**, p. 95.
- Asci grouped in a definite ascoma
 - Asci collected in a flattened, concave or closed ascoma, often bordered by a distinct layer
 - Ascoma at maturity open and more or less cup-like. **Discomycetes**
 - Ascoma open from the first, clavate or convex, pitted, or gyrose. 2. **Helvellales**, p. 99.
 - Ascoma at first closed, opening early, without special covering, more or less fleshy. 1. **Pezizales**, p. 100.
 - Ascoma opening tardily, enclosed by a tough covering which becomes torn open at the maturity of the spores
 - Ascoma roundish, opening by stellate or radiating fissures. 4. **Phacidiales**, p. 115.
 - Ascoma elongate, opening by a longitudinal fissure. 5. **Hysteriales**, p. 120.
 - Asci collected in a cylindric, globose or dimidiate perithecium
 - Perithecia sessile, solitary and free, or united and embedded in a stroma
 - Asci arranged at different levels in the perithecium
 - Not stromatic. 8. **Aspergillales**, p. 122.
 - Stromatic. 7. **Myriangiales**, p. 125.
 - Asci arising from a common level
 - Mycelium superficial, perithecia scattered, globose and without typical ostiole. 8. **Perisporiales**, p. 127.

- Mycelium not superficial, locules
 without typical ostioles... 9. *Dothideales*, p. 154.
 Mycelium immersed or superficial,
 perithecia ostiolate
 Perithecia dimidiate..... 10. *Hemisphæriales*,¹ p. 145.
 Perithecia not dimidiate
 Perithecia and stroma (if
 present) fleshy or mem-
 branous, bright colored. 4. *Hypocreales*, p. 145.
 Perithecia and stroma (if
 present) hardened, rarely
 membranous, dark col-
 ored 12. *Sphæriales*, p. 157.

Protodiscales (p. 94)

The 4-8 to many-spored asci form a flat palisade-like hymenium which arises directly from the mycelium; paraphyses none; spores, one-celled, elliptical or round.

Exoascaceæ

This family is distinguished from the other family of the order by its parasitic habit. It is the most simple of the parasitic Ascomycetes, definitely recognizable as such, and is comparable with *Exobasidium* among the Basidiomycetes. (See p. 287). All the species are parasitic and many of them injurious. The mycelium which can be distinguished from that of other fungi by its cells of irregular size and shape, wanders between the living host cells (intracellular in one species), or is sometimes limited to the region just below the cuticle. The asci develop in a palisade form on a mycelial network under the epidermis, or the cuticle, or on the ends of hyphæ arising from below the epidermal cells. They are exposed by the rupture of the cuticle or epidermis and contain four to eight hyaline, oval, one-celled spores. These by budding, while still in the ascus, may produce numerous secondary spores, conidia, which give the impression of a many-spored ascus.

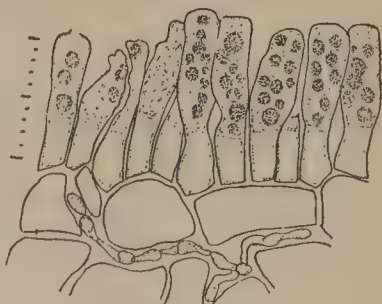


FIG. 89.—*Taphrina* showing mycelium and asci. After Atkinson.

¹ Theissen and Sydow, *Synoptische Tafeln*, Ann. Myc. **15**: 389, 1917.

The ascospores also bud freely in nutritive solutions. The primary-ascus-nucleus arises from fusion of two nuclei as is general among the Ascomycetes. The spore-nuclei arise by repeated mitoses of the primary nucleus.

Affected leaves, fruit and twigs become swollen and much distorted; wrinkled, curled, arched, puckered. In woody twigs the

mycelium often induces unnatural, profuse, tufted branching resulting in "witches brooms" though such structures often arise from irritation due to other causes.

Many attempts have been made to arrange the species in natural genera; some based on the number of ascospores,

others largely on the biologic grounds of annual or perennial mycelium. Giesenhagen whose classification is followed here, recognizes two genera, *Exoascus* being merged into *Taphrina*.



FIG. 90.—*Taphrina* showing mitoses in the young ascus leading to the development of spore-nuclei. After Ikeno.

Taphrina Fries

Mycelium annual or perennial; asci 4 to 8-spored, or by germination of the ascospores, multispored, borne on the surface of blisters and other hypertrophied areas, cylindric to clavate, or a modification thereof. Of this genus Giesenhagen recognizes four series of species which are arranged in three subgenera.

The fungus is best studied when the asci are mature but may usually be recognized by its mycelial characters.

Subgenus 1, *Taphrinopsis*, is parasitic on ferns. Subgenus 2, *Eutaphrina*, is found on Amentaceæ, chiefly *Betula*, *Alnus*, *Ostrya*, *Carpinus*, *Quercus*, *Populus*.

Subgenus 3. *Exoascus*,—two series

Asci clavate, normally cylindric or more or less abbreviated.

(1) *Prunus* series on Rosaceæ. Asci slender, clavate, narrowed below, broadest in the upper fourth, varying through all intermediate forms to narrowly cylindric.

(2) *Æsculus* series, on Sapindaceæ, Anacardiaceæ, etc.—Asci broadly cylindric, short, rounded or truncate.

The more important economic species of the genus belong to the *Prunus* series.

***T. deformans* (Fel.) Tul.**

The irregular vegetative mycelium devoid of haustoria grows in the leaf parenchyma and petiole and in the cortex of branches of the peach. A distributive mycelium lies close beneath the epidermal cells of twigs and in the pith and extends some distance through the twig. Fig. 91. Branches arise from the vegetative mycelium, penetrate between the epidermal cells to the cuticle and then branch freely to form a network of short, distended cells beneath the cuticle. This is the hymenium, a layer of ascogenous cells. These cells elongate perpendicularly to the host's surface, Fig. 89, rupture the cuticle, and form a plush-like layer. The protoplasmic contents crowd toward the tips of these cells and a basal septum cuts off the ascus proper from the stalk cell, Fig. 92.

The spores then form within the ascus. The ascospores may bud either before or after extrusion from the ascus, producing conidia, which may themselves bud indefinitely, producing secondary,

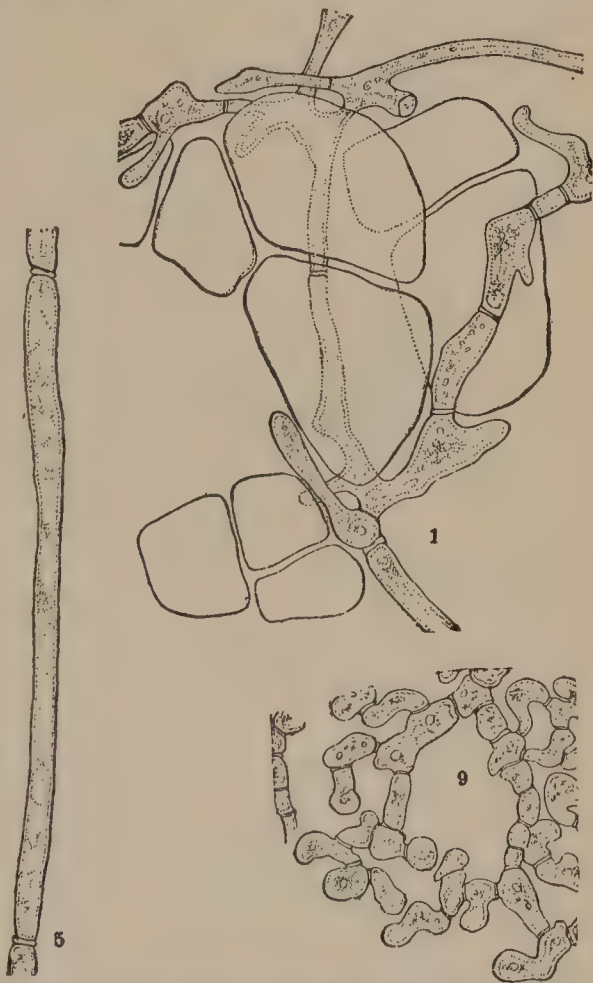


FIG. 91.—*T. deformans*. 5, distributive hypha; 1, vegetative hyphæ; 9, sporiferous hyphæ. After Pierce.

tertiary, etc., crops. In this condition the conidia strongly resemble yeast cells. On the host plant ascospores germinate by germ tubes which are capable of infecting proper hosts. No success has rewarded attempts to secure germ tubes from conidia. Leaf infection is chiefly external; rarely internal from mycelium perennating in the twigs. It occurs when the leaf is very young. Infected leaves are thickened and broadened and the tissues are

stiff and coriaceous. The palisade cells increase in size and number and lose their chlorophyll. Blistering and reddening of the leaves follows.

Asci clavate, 25–40 x 8–11 μ ; spores 8, subglobose or oval, 3–4 μ .

T. pruni (Fcl.) Tul., on plum and wild cherry; causes "plum pockets." The ovary is the seat of attack. The mycelium after bud infection pervades the mesocarp which hypertrophies and alone produces a much enlarged fruit, usually with entire sacrifice of the other fruit parts. Asci are

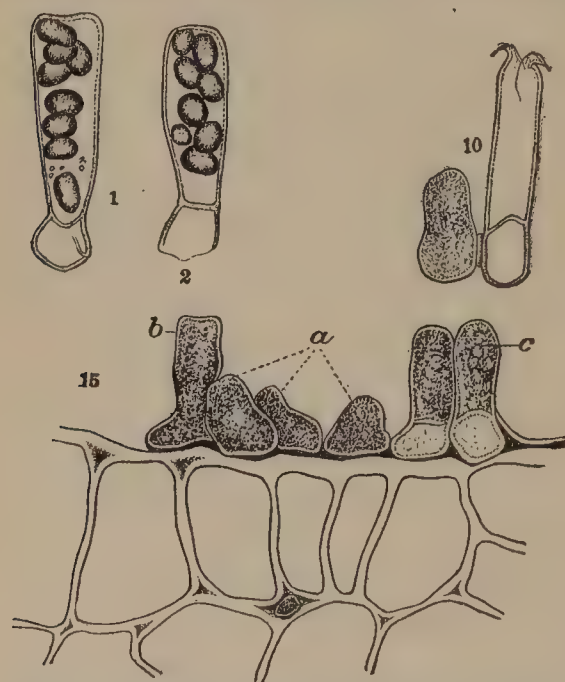


FIG. 92.—*T. deformans*. Young and old asci: 1, 2 asci with spores; 10, a young and an old ascus; 15, the young hymenial layer showing asci of various ages, a to c. After Pierce.

formed over the diseased surface much as in the last species. The mycelium is perennial in the bast and grows out into the new shoots and buds each spring. Infection also reaches other shoots and trees by means of the spores.

Ascus elongate-cylindric, 30–60 x 8–15 μ ; spores 8, globose 4–5 μ . Perennial.

T. cerasi (Fcl.) Sad. produces the witches broom effect upon cultivated and wild cherries. It is common in Europe, rare in America, perennial; asci clavate, 30–50 x 7–10 μ ; spores 8 forming conidia in the ascus, oval, 6–9 x 5–7 μ .

On *Prunus avium*, *P. cerasus*, etc.

T. communis (Sad.) Gies. Spores on immature fruits; asci clavate, $24-45 \times 5-10 \mu$; spores 8, elliptic, $5 \times 3-4 \mu$, often producing conidia.

On *Prunus americana*, *P. maritima*, *P. nigra*, and *P. pumila* producing "plum pockets." When spores infect the fruit the mycelium is at first confined to the epidermis. This fungus was thought to be perennial in the branches, but apparently often is not so since spraying gives control.

T. decipiens (Atk.) Gies., causing leaf curl, **T. farlowii** (Sad.) Gies., **T. mirabilis** (Atk.) Gies., **T. longipes** (Atk.) Gies., **T. rhizipes** (Atk.) Gies., **T. institiæ** (Sad.) Joh. are other species on *Prunus*.

T. bullata (Fcl.) Tul. is on pear and Japanese quince; **T. crataegi** (Fcl.) Sad. on *Crataegus oxyacantha*.

Helvellales (p. 94)

Ascoma fleshy, separable into a definite hymenium of asci and paraphyses; stroma usually large and stalk-like, fertile portion more or less cap-like; hymenium free from the first or covered with a thin, evanescent veil; asci cylindric, opening by an apical pore; spores ellipsoid, colorless or light yellow, smooth, or in one genus echinulate.

Rhizinaceæ

Ascocarp sessile.

Rhizina Fries

Spores elliptic or spindle-shaped, ascophores with rhizoid-like structures. Some eight species are recognized by their crust-formed, sessile, flat ascophore with root-like outgrowths from the lower side. Fig. 93. Asci cylindrical, 8-spored, opening by a lid; spores one-celled, hyaline; paraphyses many. It is often purely saprophytic, growing in burned-over forest areas.

R. inflata (Schäff.) Quel. is counted as the cause of serious root diseases of forest trees, especially conifers, in Europe.

R. undulata Fr. causes death of fir seedlings and other conifers.

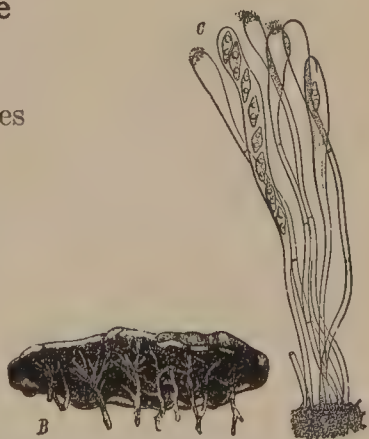


FIG. 93.—*Rhizina inflata*. B, ascocarp from below; C, asci and paraphyses. After Schröter and Tulasne.

Pezizales (p. 94)

In this order, unlike the last, the hymenium is at first enclosed but soon becomes exposed. The apothecia at maturity are typically disc or saucer shaped (Fig. 101) or sometimes deeper, as cup, beaker, or pitcher-shaped. They vary from a size barely visible up to 8-10 cm. in diameter. Some are stalked, more often they are sessile. In consistency they vary from fleshy or even gelatinous to horny. Paraphyses are present and may unite over the asci to form a covering, the **epithecium**. The apothecium may be differentiated into two layers; the upper bearing the asci is the **hypothecium**, the lower the **peridium**. In some cases sclerotia are formed. Many species possess conidiospores as well as ascospores, borne either on hyphæ or in pycnidia. The great majority are saprophytes, a few are parasitic. There are some three thousand species.

KEY TO FAMILIES OF Pezizales

- No lichenoid thallus; ascocarps free, solitary or cespitose, fleshy or waxy, rarely gelatinous; ends of paraphyses free; peridium forming a more or less differentiated membrane
- Peridium of elongate, parallel pseudo-parenchymatous, hyaline, thin-walled cells. . . . 1. **Helotiaceæ**, p. 100.
- Peridium firm, of roundish or angular, pseudo-parenchymatous, mostly dark, thick-walled cells. 2. **Mollisiaceæ**, p. 110.
- Ascocarps leathery, horny or cartilaginous; ends of the paraphyses united into an epithecium; peridium well developed, mostly leathery or horny; ascocarps at first embedded in a matrix, then erumpent, urceolate or cup-shaped, at first enclosed in a membrane which disappears later. 3. **Cenangiaceæ**, p. 114.

Helotiaceæ (p. 100)

In members of this family there is a distinctly differentiated peridium. The apothecia are usually fleshy or waxy, superficial, first closed, later opening; the paraphyses form no epithecium. Asci 8-spored. Spores round to thread-shaped, one to 8-celled, hyaline. Some of the genera are among the most serious of plant pathogens.

KEY TO GENERA OF *Helotiaceæ*

- Ascocarps fleshy, fleshy-waxy, thick or membranous
- Ascocarps fleshy-waxy, brittle when fresh, leathery when dry, not setose, springing from a sclerotium..... 1. *Sclerotinia*, p. 101.
- Ascocarps waxy, thick, tough or membranous; externally hairy, without arachnoid mycelium; spores ellipsoid or elongate; disk smooth; paraphyses obtuse at the apex.
- Walls of ascoma delicate; spores mostly 1-celled, rarely 2-celled at maturity. 2. *Dasyscypha*, p. 108.
- Walls of ascoma thick; spores 2-celled at maturity..... 3. *Lachnella*, p. 109.
- Ascocarps naked, not from sclerotia; spores ellipsoid or fusiform, 1-celled; border of disk smooth..... 4. *Hymenoscypha*, p. 109.

Sclerotinia Fuckel

This genus contains several very important pathogens, some of them preying upon a wide range of hosts and causing great loss. A striking feature of the genus is the sclerotium which is black and borne within the host tissue or upon its surface. From the sclerotia after a more or less protracted period the apothecia develop. These are disc-shaped and stalked. The asci are 8-spored; spores elliptical or fusiform, unicellular, hyaline, straight or curved. Some species possess *Botrytis* forms (see pp. 385-6), others *Monilia* (see p. 379) forms of conidial fructification. In addition to these there may be gonidia, which appear to be degenerate, functionless conidia. In some species there is no known spore form except that in the ascus.

S. ledi Naw. is of especial interest as the one fungus outside of the Uredinales that exhibits heterœcism.

Many forms found upon distinct hosts and presenting slight or even no microscopic differences, have been named as separate species. Only long careful culture studies and inoculation experiments will determine which of these species are valid, where more segregation, where more aggregation is needed.

The mere association of *Botrytis* or *Monilia* conidial forms with *Sclerotinia*, in the same host, has repeatedly led to the assumption

that such forms were genetically connected. Such assumptions are not warranted. Only the most careful study and most complete evidence justify such conclusions.

***S. cinerea*, *S. fructigena*, and *S. laxa*.**

These forms are perpetuated chiefly by their conidia. The ascus-forms are much less often seen.

When the conidia fall upon the peach, the mycelium develops and penetrates even the sound skin; then rapidly induces a brown soft rot. The mycelium within the tissue is septate, much branched, and light brown in color. It soon proceeds to form a subepidermal layer and from this the hyphæ arise in dusty tufts of *Monilia*-form conidiophores and conidia (Fig. 95). The earlier conidia are thin-walled and short lived, the later ones thicker walled and more enduring.



FIG. 94. — *S. urnula*, moniliform conidia with disjunctors. After Woronin.

After some weeks these tufts cease forming and disappear. The mycelium within the fruit persists, turns olivaceous and forms large irreg-

ular sclerotoid masses which on the following spring may produce fresh conidia.

These sclerotoid (mummified) fruits under suitable conditions in nature, usually at blossom time of the host, can also produce apothecia.

These apothecia develop in large numbers from old fruits half buried in soil, and send forth ascospores to aid in infection. The ascospores germinate readily in water and it was proved by Norton that they give rise to mycelium which produces the characteristic *Monilia*. Inoculation of ascospores on fruit and leaves also gave positive results in two or three days. The flowers, and through them the twigs, are also invaded by the mycelium which seeks chiefly the cambium and bast. Shot-hole effect is produced on leaves of peach and cherry. Infection frequently occurs through minute wounds.

On the apple the fungus shows two different modes of development. In some cases the mycelium accumulates under the epidermis without producing spores, becomes dark colored and also causes a darkening of the contents of the host cells, which results in a black spot giving rise to the name black rot. In other

cases the mycelium produces a brown rot and abundant conidial tufts, arranged in concentric circles around the point of infection.

The form on pomaceous fruits has long been regarded as identical with that on stone fruits, but recently, at least in Europe, they have been differentiated on cultural and morphological grounds, as separate species, the most distinctive character perhaps being

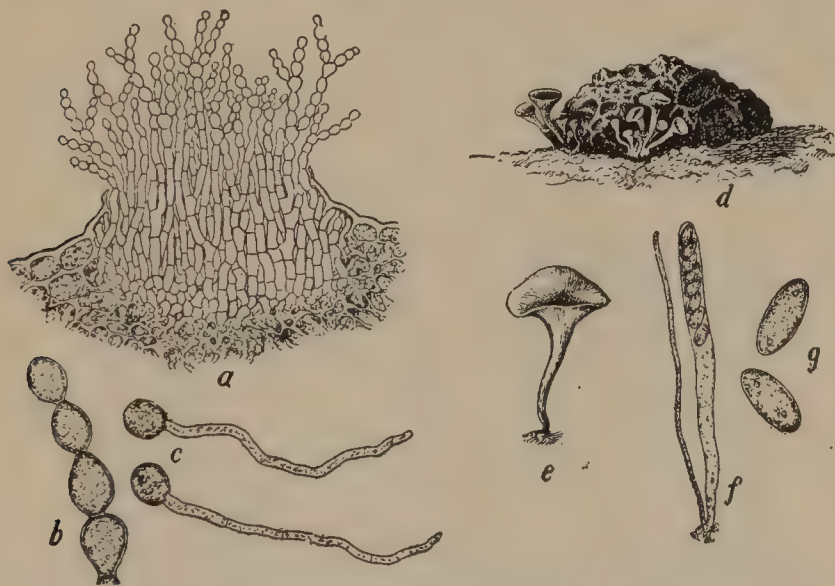


FIG. 95.—*Sclerotinia* on plum. *a*, section showing a spore pustule and chains of conidia; *b*, part of a spore-chain; *c*, spores germinating; *d*, a mummy plum and ascophores; *e*, an ascophore; *f*, ascus; *g*, mature spores. After Longyear.

the color of the mass of conidia. In a similar way *S. laxa* Ad. & Rhul. is set aside as a distinct species infecting only apricots.

From extended cultural studies Matheny concludes, "The American brown rot occurring on stone fruits is not identical with *S. fructigena* occurring in Europe on pome fruits. It agrees more nearly with *S. cinerea* and should be referred to that species."

***S. cinerea* (Bon.) Schr.¹**

Apothecia and asci similar to those of *S. fructigena*, conidia = *Monilia cinerea* Bon. Conidiophores covering the fruits with a dense, grayish mold-like growth; spores averaging $12.1 \times 8.8 \mu$. On stone and pome fruits. Cankers are also produced on spurs and branches.

¹ Matheny, W. A. A comparison of the American brown-rot fungus with *S. fructigena* and *S. cinerea* of Europe. Bot. Gaz. **56**: 418, 1913.

S. fructigena (Pers.) Schr.

Apothecia from sclerotia produced either in or on mummied fruits, 0.5–3 cm. high, stem dark brown, disk lighter, 5–8 or even 15 mm. in diameter; asci 125–215 x 7–10 μ ; spores ellipsoidal, 10–15 x 5–8 μ .

Conidia = *Monilia fructigena* Pers. Conidiophores covering the fruits of the host with a dense, mold-like growth of light brownish-yellow or ochraceous color; spores averaging 20.9 x 12.1 μ . On stone and pome fruits, especially the latter, in Europe and possibly in America.

S. seaveri, Rehm., conidia = *Monilia seaveri*, on *Prunus serotina*, causes twig blight.

S. padi Wor. is found on *Prunus padus* and *Castanea*.



FIG. 96.—*S. sclerotiorum*. Sclerotia produced in artificial culture. After Stevens and Hall.

It possesses a *Monilia*-form conidial stage with typical disjunctors, i. e., spindle-shaped cellulose bodies between the conidia which easily break across to facilitate the separation of the conidia.

S. oxycocci Wor. is on cranberry. It is unique in that half of the spores in each ascus are larger than the others. The conidial stage is a *Monilia*.

S. sclerotiorum (Lib.) Mass.=*S. libertiana* Fcl.¹

Sclerotia from a few millimeters up to 3 cm. in length, black; apothecia scattered, pale, 4–8 mm. or more broad, stem slender; asci cylindric, 130–135 x 8–10 μ , apically very slightly bluish; spores ellipsoid, usually minutely guttulate, 9–13 x 4–6.5 μ ; paraphyses clavate.

This fungus affects numerous hosts. Among the most important on which it causes serious disease are lettuce, ginseng, bean, cucumber, carrot, celery, potato, parsley, hemp, rape, lemon, various bulbs, zinnia, Columbine, Antirrhinum, petunia. The white mycelium is found superficially and within the host, especially at places where moisture is retained, as between leaves, at leaf axils, etc., also within plant cavities. Microscopically it consists of long cells branching in a rather characteristic way, Fig. 98. Within the host tissue the hyphal threads are thicker, richer in protoplasm, more septate, and much more branched and crooked than outside of the host. Aërial hyphal filaments when they touch a solid repeatedly branch in close compact fashion forming the attachment organs.

Upon the exhaustion of the food supply and the consequent termination of the vegetative period the mycelium becomes very

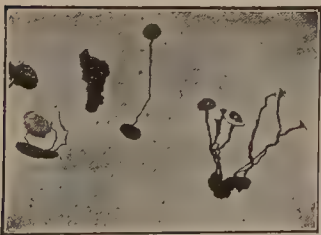


FIG. 97.—*S. sclerotiorum*. Sclerotia and apothecia. After Stevens and Hall.



FIG. 98.—Mycelium showing septation and branching. After Stevens and Hall.

dense in spots and within these clumps of mycelium the sclerotium forms; at first white, later pink, finally smooth and black (Fig. 97). They are often found in the leaf axils (lettuce), in the pith of stems (carrot), etc. Under some conditions, as on unsuitable nutrient media, gonidia are produced.

The sclerotia can germinate at once or remain dormant for one, perhaps several years. On germination they send forth

¹ Wakefield, E. M. On the names *Sclerotinia sclerotiorum* (Lib.) Massee, and *S. libertiana* Fuckel. *Phytop.* **14**: 126, 1924.

from 1 to 35 negatively geotropic sprouts which grow to the soil surface unless that be more than about 5 cm. distant. On reaching the light the apex of the sprout thickens and soon develops its apothecium; at first inverted-conical, soon flat, and finally somewhat revolute. Changes in atmospheric humidity cause the discharge of ascospores in white clouds.

The ascospores germinate readily but the resulting mycelium is of such small vigor that it is incapable of parasitism. If the ascospore germinates where it can maintain a saprophytic life until a vigorous mycelium is developed then the mycelium may become parasitic.



FIG. 99.—*S. sclerotiorum*, asci and paraphyses. After Stevens and Hall.

Both ascospores and mycelium are comparatively short-lived. The mycelium can migrate but a short distance over soil. No form of conidia except the apparently functionless gonidia is produced.

It has been repeatedly claimed that this fungus possesses a *Botrytis* conidial stage, but the results of much careful work deny this.

Tests by Westerdijsk indicate the absence of such biologic specialization in regard to hosts as is found in *Erysiphe* and elsewhere.

***S. perplexa* Lawrence¹**

Ascophores rare to very numerous and dense, naked, smooth, pale flesh colored, saucer-shaped, stipitate, 2–8 mm. broad, stipe 1–2 mm. long; asci cylindrical, 115–145 x 5–7 μ , 8-spored; spores elliptical, hyaline, 1-celled, 8–10.5 x 3.5–5 μ ; paraphyses simple, slender, cylindrical, non-septate; sclerotia grey, later dull black, snow-white within, to pink or brown with age, round, 1–3 mm. in diameter or smaller, tuberiform, or forming thin, black crusts, 1–115 mm. in length, giving rise to ascophores or conidiophores or both; conidiophores densely tufted and woolly, greyish brown, straight and uniform below, slightly irregular above, 2–3–10 mm. tall, dichotomously and sparingly forked, the branches long and wide-angled, conidia broadly obovate, or elliptical, slightly truncate at base, 8–15 x 6–10 μ .

The cause of rot of Jerusalem artichoke, sunflower, onion, cucumber, chicory, cabbage, rutabaga and other crucifers.

¹ Lawrence, W. H. Plant diseases induced by *Sclerotinia perplexa* n. sp. Wash. Agr. Exp. Sta. Bull. 107, 1912.

S. ricini Godfrey. Apothecia one to several from a single sclerotium, 5-30 mm. high, infundibuliform to cyathiform and discoid, long stipitate, cinnamon brown to chestnut brown, disc at first closed, expanding to saucer-shaped with margin sometimes recurved, exterior roughened, 1-7 mm. in diameter; asci cylindrical to cylindro-clavate, apex slightly thickened, opening by a pore, $50-110\ \mu \times 6-10\ \mu$; spores 8, ellipsoidal, hyaline, continuous, biguttulate, $9-12 \times 4-5\ \mu$; paraphyses abundant, filiform, septate, hyaline, $1.5-2\ \mu$ in diameter. Conidial stage (*Botrytis* sp.) forming a widespread cobwebby or somewhat woolly mass, pale drab-gray; sterile hyphæ procumbent, hyaline, many-septate, often vacuolate, frequently anastomosing, fertile hyphæ long, slender, smooth, slightly constricted at the base, olivaceous when mature, dichotomously branched; conidia borne on sterigmata, globose, smooth, hyaline, $6-12\ \mu$, compactly grouped; microconidia globose, hyaline, $2-3.5\ \mu$, borne apically on short conidiophores that develop on the sides of hyphæ or on tips of special branches; appressoria rare, $20-60\ \mu$ across base. Sclerotia black, rough, elongate, irregular, 1-25 mm. in length.

Parasitic on *Ricinus communis*, usually on inflorescences, also on stems and leaves.

S. minor Jagger.¹ Apothecia one, rarely more, from a sclerotium; disk 0.5-2 mm. in diameter; asci $125-175 \times 8-11\ \mu$, 8-spored; spores $5-9 \times 8-20\ \mu$. Paraphyses filiform; gonidia globose, hyaline, $3-4\ \mu$, on short, obclavate conidiophores; sclerotia black, 0.5-2 mm. in diameter.

Parasitic on lettuce and celery. The decay is similar to that produced by *S. sclerotiorum*.

S. smilacina Dur., = *S. panicis* Rankin, is described as parasitic on the rhizomes of ginseng causing a black rot. Sclerotia 0.3-1 cm. black; asci $125-137 \times 6.4\ \mu$; spores $11.7-16 \times 4.8-7.5\ \mu$.

S. nicotianæ Oud. & Kon. parasitizes the leaves and stems of tobacco. It is possibly identical with *S. sclerotiorum*.

¹ Jagger, J. C. *Sclerotinia minor*. n. sp. The cause of a decay of lettuce, celery and other crops. Jour. Agr. Res. **20**: 331, 1920.



FIG. 100.—Cultures of *Sclerotinia* from tobacco on potato agar, showing sclerotia. After Clinton.

S. trifoliorum Erik.

In general this resembles *S. sclerotiorum* with which it is by some regarded as identical. The sclerotia, varying in size from that of a mustard seed to a pea, are found in the decayed tissue, or as larger, flat, surface sclerotia. There are no conidia except the functionless gonidia. On clover and alfalfa.

S. bulborum (Wak.) Rehm, which is very similar to *S. trifoliorum* and without known conidia, grows on hyacinth, crocus, scilla and tulip. Cross infections between hyacinth and clover have not been successful and the species may be distinct.

Several other species of the genus are found on Ericaceæ, Betulaceæ, Rosaceæ, Gramineæ, etc.

Dasyscypha Fries (p. 101)

This is a genus of some one hundred fifty species, mostly saprophytic but, sometimes parasitic on twigs. The apothecia are small, short-stalked or sessile, waxy or membranous, bright colored in the disk, with mostly simple hairs on the outside and margin. Asci cylindrical or clavate, 8-spored; spores ellipsoid or fusiform, hyaline, 1-celled, rarely 2-celled, sometimes guttulate; paraphyses blunt, needle-like.

D. willkommii Hart. causes a serious larch disease and affects also the pine and fir.

The stromata appear as yellowish-white pustules on the bark soon after its death. Here hyaline conidia are produced on the open surface or in cavities. Apothecia

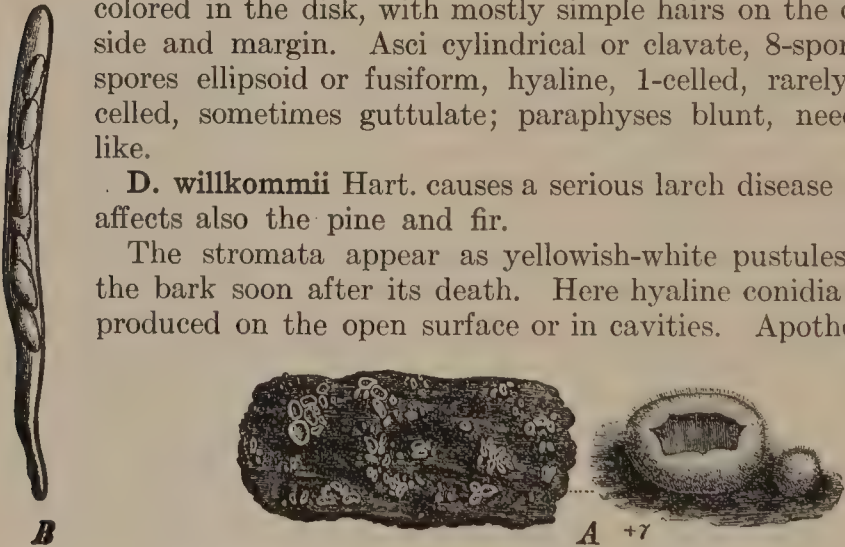


FIG. 101.—*D. willkommii*. A, natural size and single apothecium enlarged; B, an ascus. After Lindau.

2–5 mm. broad appear later. The ascospores can infect wounds; the conidia seem to be functionless. The mycelium spreads through the sieve tubes, intercellular spaces, and xylem to the pith.

Apothecia short-stalked, yellowish without, orange within; asci $120 \times 9 \mu$; spores $18\text{--}25 \times 5\text{--}6 \mu$; paraphyses longer than the ascus.

D. resinaria Rehm is a wound parasite much like the above in its effects. It occurs chiefly on spruce and larch but sometimes also on pine.

Ascophores upon cankers on branches and trunk of the host are very similar to those of the preceding species but with more evident stipe and paler disk; spores very minute, subglobose, $3 \times 2-2.5 \mu$; conidia $2 \times 1 \mu$.

Other species are found on spruce, pine, and other conifers.

Lachnella Fries (p. 101)

This is similar to the last genus but with the apothecia usually sessile and the spores usually 2-celled at maturity, and in two rows in the ascus. There are about forty species.

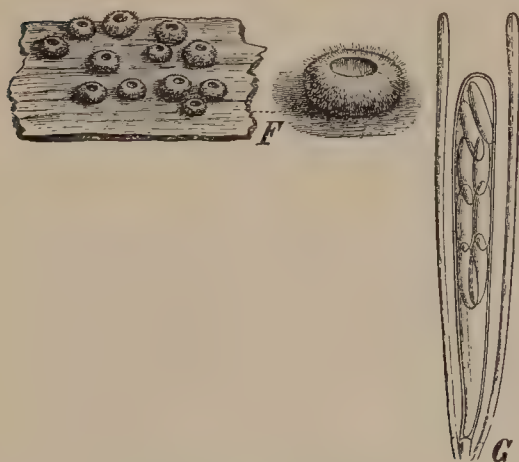


FIG. 102.—*Lachnella*. *F*, habit sketch; *G*, ascus and paraphyses. After Rehm.

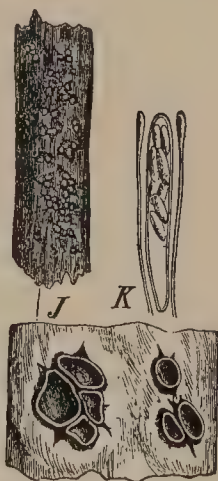


FIG. 103.—*Hymenoscypha*. *J*, habit sketch; *K*, ascus and paraphyses. After Rehm.

L. pini Brun. injures pine twigs. The apothecia are brown outside; the disc reddish-yellow with a white margin.

Ascoma short-stipitate, 5 mm. in diameter, pale brown; disk light orange-red with a pale margin; asci $109 \times 8-9.5 \mu$; spores $19-20 \times 6.5-8.5 \mu$, hyaline.

Hymenoscypha Fries (p. 101)

This genus of over two hundred species is mainly saprophytic. Ascoma sessile or short-stipitate, usually smooth; asci cylindric

to globoid, 8-spored; spores elliptic, blunt to pointed, hyaline; paraphyses filamentous, apically enlarged, hyaline.

H. tumultenta P. & D., in its conidial stage as *Endoconidium*, affects rye grain causing it to shrivel and assume poisonous properties. The conidia are borne endogenously in the terminal branches of the hyphæ and escape through an opening in the end of the branch.

Mollisiaceæ (p. 100)

Ascocarp fleshy, waxy, are rarely membranous, bright colored, at first sunken in the substratum and later slightly erumpent, at first more or less globose, becoming flattened; asci 8-spored, opening by a slit; spores hyaline, 1 to many-celled; paraphyses slender. There are above four hundred species.

KEY TO GENERA OF THE Mollisiaceæ

Ascocarps bright colored, only slightly erumpent

Spores ellipsoid or elongate, rounded, 1-celled 1. **Pseudopeziza**, p. 110.

Spores becoming 2 to 4-celled

Apothecium developed within or on an exposed stromatic subiculum..... 2. **Neofabræa**, p. 111.

Apothecium on a covered subiculum..... 3. **Fabræa**, p. 112.

Ascocarps dark colored, at length strongly erumpent; externally smooth, the margin at most merely shredded; spores ellipsoid or fusiform, 1-celled.....

4. **Pyrenopeziza**, p. 113.

Pseudopeziza Fuckel

The genus comprises some ten species, all parasitic on leaves, several of them upon economic plants causing serious disease. The very small apothecium develops subepidermally breaking through only at maturity, light colored; spores 1-celled, hyaline, in two ranks in the ascus; paraphyses somewhat stout, hyaline. Conidial forms are found in *Gloeosporium*, *Colletotrichum* and *Marssonina*.

P. medicinis (Lib.) Sacc.

The epiphyllous apothecia are in the older leaf spots, subepidermal at first but eventually breaking through.

Apothecia saucer-shaped, light colored, fleshy; asci clavate; spores hyaline, 10–14 μ long; paraphyses numerous, filiform.

On dead spots in leaves of alfalfa and black medick.

***P. trifolii* (Bernh.) Fcl.**

This species on *Trifolium* is closely related to, perhaps identical with, the last species.

***P. ribis* Kleb.**

Apothecia appear in the spring on dead leaves of the previous season; saucer-shaped, fleshy, somewhat stalked; asci clavate, spores hyaline, ovoid; paraphyses simple or branched, slightly clavate, rarely septate.

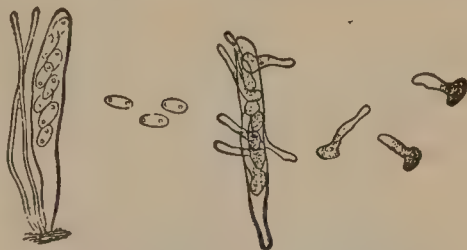


FIG. 104.—*P. trifolii*. Ascus and paraphyses; germinating spores. After Chester.

Conidial phase (= *Glœosporium ribis*) on the leaves of the host forming an abundant amphigenous infection; acervuli stromatic; conidiospores commonly $19 \times 7 \mu$, varying from $12\text{--}24 \times 5\text{--}9 \mu$, escaping in gelatinous masses.

On red and white currants, less commonly on black currants and gooseberries.

The ascigerous stage of this fungus was demonstrated by Klebahn in 1906 to be genetically connected with what had been earlier known as *Glœosporium ribis*. Old leaves bearing the latter fungus were wintered out of doors in filter paper and in the spring an ascigerous stage was found. The ascospores were isolated, grown in pure culture and typical conidia were produced. The ascospores also infected the host leaves successfully, producing there the typical *Glœosporium*. The conidial stage is the only one ordinarily



FIG. 105.—*P. ribis*. Apothecium in section. After Klebahn.

seen. The acervuli are subepidermal elevating the epidermis to form a pustule which eventually ruptures and allows the spores to escape as a gelatinous whitish or flesh-colored mass. The spores are curved and usually larger at one end than at the other.

***Neofabræa* Jackson¹ (p. 110)**

Characteristics in general those of *Pseudopeziza*; apothecia developing in, and at length breaking forth from, a more or less ex-

¹ Jackson, H. S. Ore. Agr. Exp. Sta. Bienn. Crop Pest Hort. Rept. 1911-12, 178.

posed subiculum consisting of the old conidia-bearing stroma. Spores at first one-celled; at length two to four celled.

N. malicorticis (Cordley) Jackson

Apothecia 0.5–1 mm. in diameter, light brown, waxy, at first concave, then flat and finally convex, surrounded at the edge with

the black remains of enveloping layers. Developing within and bursting forth from a subiculum consisting of the old conidia stroma. Asci clavate, 90–100 μ long, 10.5–13 μ broad; spores colorless, one-celled or becoming four-celled on germination, 16–19 μ long by 5–7 μ broad, elliptical, slightly flattened on one side, uniseriate; paraphyses simple or branched, septate, tips slightly swollen. Developing in the autumn in cankers formed during the previous season.

Conidia (= *Glœosporium malicorticis*).

Caulicolous; spots brownish, slightly depressed, irregular in outline; acervuli minute, erumpent; conidia elliptic, curved,

hyaline or greenish-tinged, granular, 24 x 6 μ .

On apple and quince branches and twigs causing canker, also on fruit causing rot.

The spots begin in the bark in autumn, soon reaching to the cambium where they extend rapidly, the fungus reaching to some extent into the sap and even the heartwood. In the following midsummer acervuli appear.

Fabræa Saccardo (p. 110)

This genus of small leaf parasites much resembles *Pseudopeziza* but differs from it in its 2 to 4-celled spores; paraphyses hyaline.

F. maculata (Lev.) Atk.

The perfect stage is common on pear and quince leaves which have wintered naturally. When such leaves are wet, the white

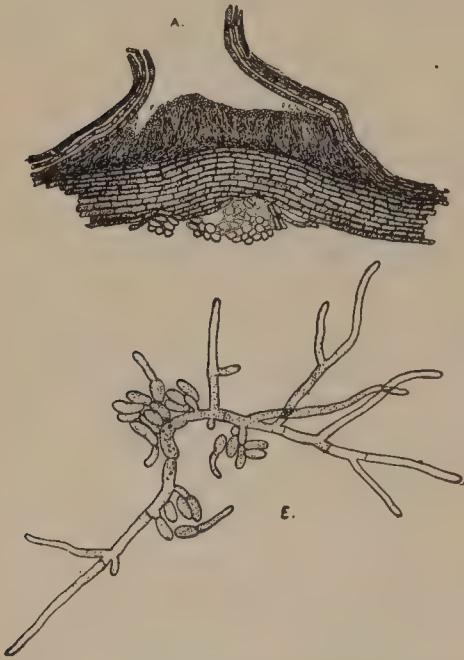


FIG. 106.—*N. malicorticis*; a, acervulus; E, germinating spore. After Cordley.

8-spored asci may be seen crowding through the surface in small elliptical areas. The apothecium is paraphysate; the spores hyaline and 2-celled.

Conidial form (= *Entomosporium maculatum*) on leaves and fruits; aceruvli, black, subepidermal, the epidermis breaking away to expose the spore mass; spores hyaline, $18-20 \times 12 \mu$, 4 cells in a cluster, the lateral cells smaller, depressed; stipe filiform, $20 \times 0.75 \mu$; the other cells with long setæ.

Atkinson proved the connection of the ascigerous with the conidial form by cultivating the conidia from the ascospores. The conidial form is very common and destructive on pear and quince leaves and fruit. The mycelium which abounds in the diseased spot is hyaline when

young, dark when old. It collects to form a thin subcuticular stroma. On this the spores are produced on short erect conidiophores, Fig. 107; eventually the cuticle ruptures and the spores are shed. The spores germinate by a tube which arises near the base of a bristle.

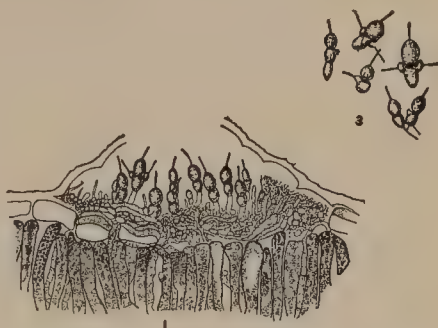


FIG. 107.—*F. maculata*. 1, acervulus of conidial stage in section; 3, spores. After Southworth.

***Pyrenopeziza* Fuckel (p. 110)**

***P. medicaginis* Fcl.¹**

Apothecia sessile on stromata, 0.25–1 mm. in diameter, outer wall black; paraphyses $50-80 \times 2.5-3 \mu$; asci $60-70 \times 10 \mu$; spores ovoid, $8-11 \times 5-6 \mu$.

Conidia (= *Sporonema phacidioides* Fcl.) in acervuli; conidiophores bottle-shaped, $12-14 \times 3 \mu$; conidia cylindrical, slightly bent, $5-9 \times 2-3 \mu$.

On alfalfa causing yellow leaf spots. The mycelium is both inter- and intracellular, in late stages filling the parenchyma cells. The acervuli develop subepidermally in the living host tissue; the ascigerous stage on dead tissue. Inoculations with ascospores gave positive results in about two weeks, but conidia failed to do so.

¹ Jones, F. R. Yellow-leaf blotch of alfalfa caused by the fungus *Pyrenopeziza medicaginis*. Jour. Agr. Res. **13**: 307, 1918.

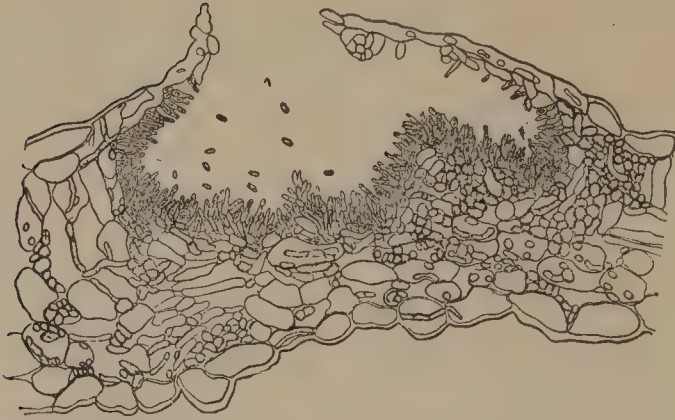


FIG. 108.—Conidial stage of *P. medicaginis*. After Jones.

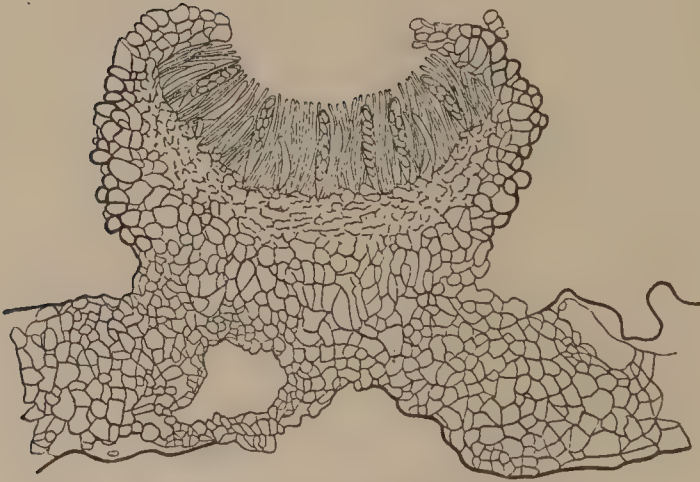


FIG. 109.—*P. medicaginis*, section showing asci. After Jones.

Cenangiaceæ (p. 100)

Ascoma at first buried, later erumpent, on a stroma, dark, with a rounded or elongate disk; asci 8-spored; spores long or filiform, 1 to many-celled, often muriform, hyaline or dark; paraphyses branched forming a complete epithecium. About two hundred fifty species.

Cenangium Fries

Parasitic or saprophytic, chiefly in bark, the apothecium developing subepidermally and later breaking through to the surface; sessile, light colored without, dark within; asci cylindric-globoid, 8-spored; spores ellipsoid, 1 or rarely 2-celled, hyaline or brown, in one row; paraphyses colored. About seventy species.

C. abietis (Pers.) Duby causes serious injury to pine.

Ascoma dark-brown, erumpent, clustered; spores ellipsoid, $10-12 \times 5-7 \mu$.

Conidia (= *Brunchorstia destruens* Erik.) in pycnidia which are partially embedded in the host, the smaller simple, the larger compound, 1–2 mm. in diam.; spores $30-40 \times 3 \mu$, tapering-rounded at each end, 2 to 5-septate.

A second conidial phase (= *Dothichiza ferruginosa* Sacc.) has simple spores.

C. piniphilum Weir.

Apothecia appearing singly, then in groups, rupturing the epidermis, coriaceous, membranaceous, 2–5 mm. across, carbonous; disc brownish to black, surface velvety or wrinkled; asci clavate, rounded above, long stipitate, averaging $135.8 \times 14.1 \mu$, 8-spored; spores irregularly 2-seriate, oblong to ellipsoid or fusiform, extremities acute, hyaline, continuous, averaging $18.9 \times 6.4 \mu$; paraphyses filamentous, branched, longer than the asci, hyaline. On pine. The mycelium penetrates the cortex, phloem, and wood causing canker.



FIG. 110.—*Cenangium*, habit sketch, asci and paraphyses. After Tulasne.

Phacidiales (p. 94)

This order, comprising some six hundred species only a few of which are pathogens, is characterized as follows: mycelium well developed, much branched, multiseptate; ascocarps fleshy or leathery, free or sunken in the substratum or in a stroma, rounded or stellate, for a long time enclosed in a tough covering which at maturity becomes torn; paraphyses usually longer than the asci, much branched, forming an epithecium.

Phacidiaceæ

Apothecia sunken, more or less erumpent, disk-like or elongate, single or grouped, leathery or carbonous, black, firm, opening by lobes or rifts; hypothecium thin, poorly developed.

KEY TO GENERA OF Phacidiaceæ

- Apothecia firmly united to the substratum II. **Phacidieæ**.
 Apothecia separate, no stroma
 Spores ellipsoid or globoid, 2 to 4-celled,
 brown 1. **Keithia**, p. 116.
 Spores filiform or needle-like, 1 to many-
 celled 2. **Coccomyces**, p. 117.
 Apothecia collected on a stroma, opening elon-
 gate, spores 1-celled, hyaline, filiform or
 needle-like 3. **Rhytisma**, p. 119.

Keithia Saccardo

Ascoma erumpent, disk black, asci 8-spored, paraphysate. Spores 1-septate, ellipsoid-ovate, brown.

K. thujina Dur.

Ascoma epiphyllous, erumpent, at first buried beneath the epidermis which is lifted up, breaks around the margin, and finally falls away as an entire flap or scale, exposing the ascoma in the form of a cushion-like elevation. Ascoma circular to elongate-elliptic, straight or curved, convex above, 0.5 mm. broad, 1.25 mm. long: disk olive to olive-brown. Asci clavate, stout, 80–100 x 18–20 μ , opening by a pore. Spores 2, at first hyaline, finally olive-brown, broadly ellipsoid or piriform-ellipsoid, at first continuous, finally divided by a single transverse wall close to the distal end into very unequal cells, epispore with minute pits over its whole surface, 22–25 x 15–16 μ . Paraphyses branched below, septate, strongly clavate-thickened in the distal third, olive colored. The cause of black leaf spot of arbor-vitæ.

K. tsugæ (Farl.) Dur.

Ascomata hypophyllous, numerous, scattered, minute, at first buried beneath the epidermis which is finally ruptured and turned to one side as a scale, dark brown, orbicular to elliptic, 0.3–0.5 mm. in diameter. Asci oblong-clavate, apex rounded, 58–65 x 13–16 μ . Spores 4, uniseriate, at first hyaline, finally greenish-brown, ellip-

soid-ovoid, divided by one septum into two unequal cells of which the proximal is smaller, constricted at septum, $13-16 \times 6-8 \mu$, smooth. Paraphyses cylindric, septate, hyaline below, the tips clavate, olive-brown, $4-5 \mu$ thick.

On hemlock.

Coccomyces DeNot (p. 116)

C. hiemalis Higgins

Ascocarps embedded in the tissue of the leaf, usually filling the entire space between the lower and the upper epidermis. Ovate to orbicular, dark brown or black. At maturity opening by irregular stellate slits on the under side of the leaves, $125-210 \mu$ in diameter; asci 8-spored, $70-95 \times 11-14 \mu$; paraphyses filiform, septate, apex slightly enlarged, often hooked or forked; ascospores linear, $33-50 \times 3.5-4.5 \mu$, continuous or 1 to 2-septate; apothecial conidia produced on short conidiophores in apothecia after shedding of ascospores, long, slender, $50-80 \times 2.5-4 \mu$, curved, continuous or 1 to 2-septate.

Conidial stage (= *Cylindrosporium hiemalis*): Mycelium intercellular with small haustoria which penetrate the host cells; acervuli amphigenous, subepidermal, finally erumpent, exposing the spores; conidia elongate, curved or flexuous, $45-65 \times 2.5-4 \mu$, continuous or 1 to 2-septate; microconidia (spermatia?) produced in same acervulus in late summer and fall, small, continuous $4-5 \times 1.55 \mu$.



FIG. 112.—*Coccomyces* on *Prunus*, haustoria in the mesophyll surrounded by cellulose sheaths. After Higgins.



FIG. 111.—*Coccomyces* on *Prunus*, young haustoria in leaf cells. After Higgins.

Conidial stage parasitic in leaves of *Prunus avium*, *P. cerasus*, and *P. pennsylvanica*. Ascigerous stage saprophytic, appearing the last of April to June, on fallen leaves of the same hosts following the conidial stage.

C. prunophoræ. Higgins. Ascocarps hypophyllous, usually aggregated, subepidermal, erumpent, $125-250 \times 100-160 \mu$, black, at maturity opening in a stellate manner; asci $63-87 \times 9-12 \mu$; spores slender, straight, curved near the end, $40-60 \times 2.5-3.5 \mu$, continuous or 1 to 3-septate; paraphyses simple or branched, enlarged at apex, septate, apothecial conidia produced on short conidiophores inside the apothecia, following

the asci, usually 1-septate, $40-60 \times 2.5-3.5 \mu$, resembling ascospores, but usually stouter.

Conidial stage (= *Cylindrosporium prunophoræ*): Mycelium intercellular with haustoria which enter host cells; acervuli subepidermal, amphigenous, finally breaking through exposing the white mass of spores, conidia elongate, slender, straight or curved, $46-65 \times 3.5-5 \mu$, usually 1-septate; microconidia (spermatia?) found in same acervuli in late summer, small, continuous $4-5 \times 1.5 \mu$.

Conidial stage parasitic in leaves of plums, *P. domestica*, *P. insititia*, *P. americana* and probably *P. spinosa*. Ascigerous stage saprophytic on fallen leaves of the same hosts.

C. lutescens Higgins. Ascocarps hypophyllous, subepidermal, erumpent, $130-300 \times 70-150 \mu$, opening in an irregular manner, asci clavate, $70-80 \times 14-19 \mu$; spores elongate, fasciated in end of ascus, $40-51 \times 3.5-4.5 \mu$, continuous or occasionally once or

twice septate; paraphyses usually simple though occasionally branched, slightly enlarged at tip; apothecial conidia very long, $58-87 \times 3.5-5 \mu$, 1-septate with usually a single vacuole in each cell.

Conidial stage (= *Cylindrosporium lutescens*): Mycelium intercellular, with haustoria which penetrate the host cells, acervuli subepidermal, amphigenous; conidia exuding in masses or in long tendrils from the break in the host epidermis, long, slender, $50-87 \times 3.5-5 \mu$, continuous, 1 to 3-septate, microconidia (spermatia?) produced in the same acervuli in late summer, small, continuous, $4-5 \times 1 \mu$.

Conidial stage parasitic in leaves of *P. serotina* and in leaves and fruits of *P. virginiana* and *P. mahaleb*. Ascigerous stage saprophytic on fallen leaves of the same species.



FIG. 113.—*Coccoomyces* on *Prunus*, showing enlargement of a layer of cells and their final separation causing the fall of the diseased tissue. After Higgins.

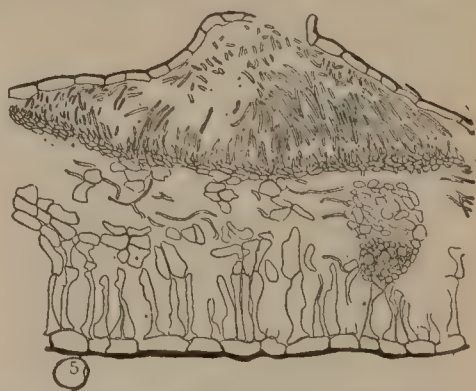


FIG. 114.—*Coccoomyces* on *Prunus*. An acervulus showing the thin stromatic layer. After Higgins.

The three closely related species given above cause the "shot holes" in leaves of the genus *Prunus* so long attributed to the species *Cylindrosporium padi* described by Karsten in 1884.

The mycelium (on *P. virginiana*) is intercellular with haustoria which penetrate the host cells; Fig. 112. The host cells are not killed at first and apparently die eventually from drying rather than from toxic action.

The absciss layer causing the "shot holes" is produced by the rapid enlargement of a layer of cells at some distance from the ends of the mycelium. Fig. 113. The structure of the acervulus and of the ascocarp is shown in Figs. 114, 115. Positive inoculations have been secured both by conidia and by ascospores.

***C. pini* (Alb. & Schw.) Karst.¹**

Ascocarp emergent, laciniate-dehiscent, disc. 1.5–4 mm. broad; asci long-pedicellate, 100–130 x 10–15 μ , 8-spored; spores filiform, clavate, 5 to 9-septate, 65–80 x 3–4 μ ; paraphyses filiform; conidial stage (= *Cylindrosporium* sp); spores filiform, hyaline, continuous, 10 x 1 μ .

On white pine causing blight of the bark on twigs.



FIG. 115.—An ascocarp of *C. hienalis* on its thick stroma. After Higgins.

***Rhytisma* Fries (p. 116)**

To *Rhytisma* belong about 70 species which cause very conspicuous, though but slightly injurious, black leaf spots. The spots, which are white within, are due to sclerotial cushions formed in the host tissue. Thickening of the leaf occurs in the infected part. One-celled conidia are abundantly produced in pycnidia early in the season, followed by sclerotium formation. Much later, usually well into winter or the following spring, the apothecia appear. Besides the ascospore-producing forms several species of which the ascospores are unknown have been referred here.

Ascoma on a sclerotial stromatic layer, which is black above, white within; ascocarps elongate, opening by a lip-like slit; asci clavate, often blunt pointed, 8-spored; spores filiform or needle-

¹ Graves, A. H. Notes on diseases of trees in the southern Appalachians. *Phytop.* 3: 129, 1913.

like, hyaline, mostly 1-celled, lying parallel and lengthwise of the ascus; paraphyses filiform, hyaline, often arched above.

R. acerinum (Pers.) Fr.

The spot is at first yellow and thickened and in this stage bears numerous conidia upon short conidiophores. The apothecia ripen in spring and rupture by numerous irregular fissures which follow the ridges of the wrinkled surface. Klebahn secured infection by ascospores resulting in three weeks in yellow spots and in eight weeks in conidiospores. The conidia are supposed to aid in spreading the fungus during the summer.

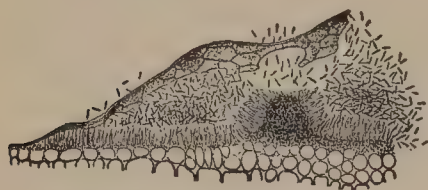


FIG. 116.—*R. acerinum*; conidial layer.
After Tulasne.

on the stroma which is about 0.5–1.5 cm. across; asci 120–130 x 9–10 μ ; spores large, 65–80 x 1.5–3 μ ; paraphyses numerous, incurved or hooked.

Conidia (= *Melasmia acerina* Lév.) preceding the asci, producing numerous, small, hyaline, 1-celled spores in an extended hymenial layer.

On various species of maple, consisting of biologic races.

R. punctatum (Pers.) Fr. also occurs on maple. It may be distinguished from the preceding by its small, speck-like stromata.

R. salicinum (Pers.) Fr., found on willow, is quite similar in external appearance to *R. acerina*.

R. symmetricum Müll. is another willow inhabiting species.



FIG. 117.—*Rhytisma*. Ascus and paraphyses.
After Rehm.

Hysteriales (p. 94)

Small species with elongated, black, covered apothecia which open by a long narrow slit exposing the hymenium; asci 8-spored; spores usually long and slender. Some few are leaf parasites but most are wood saprophytes. Pycnidia are found in some species. The order serves as a bridge between the Discomycetes and the Pyrenomycetes.

Hypodermataceæ

Ascocarp flattened, rounded or elongate, rarely branched, immersed, united to the substratum; opening by a slit; asci 4 to 8-

spored; paraphyses apically branched, the branches forming an epithecium, or hooked or crimped.

KEY TO GENERA OF *Hypodermataceæ*

Spores elongate, rather broad

Spores 1-celled, hyaline, asci 4-spored . . . 1. *Hypodermella*, p. 121.

Spores 2-celled, hyaline, apothecium black 2. *Hypoderma*, p. 121.

Spores filiform, 1-celled 3. *Lophodermium*, p. 122.

Hypodermella Tubeuf

This differs from the next genus in its pyriform, unicellular spores; asci 4-spored.

H. larius Tub. occurs on larch.

Hypoderma De Candolle

Apothecia oblong, opening through a thin black cover by a long fissure; asci 8-spored; spores cylindrical or fusiform, 2-celled at maturity; paraphyses hooked at the end.

H. desmazieri Duby is found on pine needles.

Amphigenous; asci broadly clavate, sessile; spores hyaline, linear-elliptic, obtuse and 2-rowed.

H. laricis, and *H. pinicola*, produce premature leaf fall in various conifers.

H. deformans Weir.¹

Apothecia black, shiny, averaging 10 mm. in length and 1 mm. in breadth; opening with a longitudinal medial split. Asci fusiform, 8-spored, 26–43 x 159–207 μ . Spores parallel or obliquely arranged in the ascus, generally slightly curved, rod-shaped, ends blunt, 1-septate when mature, septum conspicuous, cells often apparently separated, pale

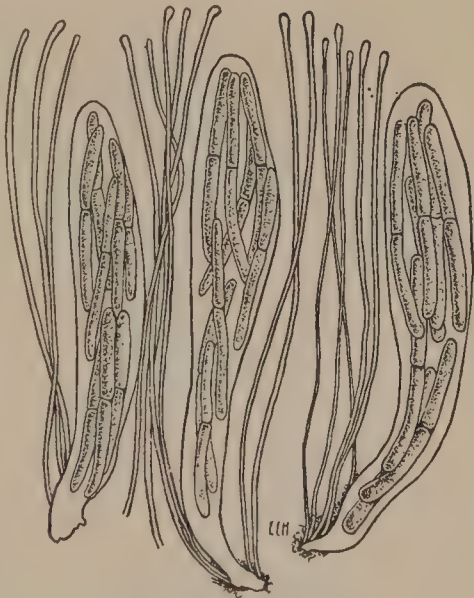


FIG. 118.—Asci, spores, and paraphyses of *Hypoderma deformans*. After Weir.

¹ Weir, James R. *Hypoderma deformans*. An undescribed needle fungus of the western yellow pine. Jour. Agr. Res. 6: 277, 1916.

olive, almost hyaline, $6-10 \times 90-131 \mu$; paraphyses numerous, filamentous, swollen at the ends or recurved. Spermatia elongate, straight, sometimes slightly curved, hyaline, continuous, averaging $1 \times 8 \mu$.

On pine needles causing their death. The fungus also reaches into the twigs causing hypertrophy and preventing proper development of the terminal shoots.

Lophodermium Chevallier (p. 121)

Spores long, thread-like, continuous; conidiospores in pycnidia.

L. pinastri (Schr.) Chev. occurs on *Pinus sylvestris* especially on young plants causing the leaves to fall. The first year pycnidia only are formed, the asci not appearing until the second year.

Ascocarps scattered on the leaf, shining black, up to 1 mm. long; asci clavate, 8-spored; spores nearly as long as the ascus, $90-120 \times 1.5 \mu$. Conidia cylindric, hyaline, continuous, $6-8 \times 1 \mu$.

L. brachysporum Rost. = *Hypoderma strobicola* Tub.

Perithecia epiphyllous; asci cylindric, short-stalked, apex rounded, $120 \times 20-25 \mu$; 8-spored; paraphyses bacillar, apex curved; spores oblong, 1-rowed, hyaline, $28-30 \times 9-10 \mu$.

It is common on pine leaves.

Several other species are parasitic upon various conifers, among them: **L. nervisequum** (DC.) Fr. on fir leaves, causing defoliation and death; perhaps identical with *Hypoderma desmazieri* Duby.

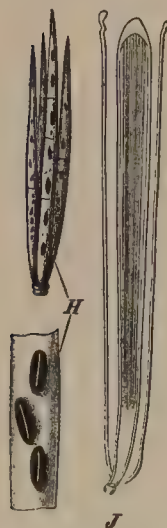


FIG. 119.—*L. pinastri*.
H, habit sketch; J,
ascus and paraphyses.
After Rehm.

Aspergillales (p. 94)

The Aspergillales are clearly distinguished from the other Ascomycetes by the possession of a closed, astromate ascocarp, in which the asci are not collected in a hymenium but are irregularly scattered. The forms with the least developed peridium are evidently related to the Endomycetaceæ; the forms with a more highly developed peridium, to the Pyrenomycetes, particularly to the Perisporiales. Conidial forms are usually present, indeed in many cases they preponderate almost to the entire exclusion of

the ascigerous form which may be seen only under very exceptional conditions.

Sexual reproduction has been demonstrated in several families. In the Gymnoascaceæ there are usually two twisted branches which conjugate. These branches are multinucleate at the time of fusion. The ascogonium develops from this fertilization much as is described on pages 89, 90. In the Aspergillaceæ similar sexual organs are formed but parthenogenesis or a much reduced form of fertilization is often met.

Aspergillaceæ

The ascocarp, in many forms but rarely seen, is a small spherical or tuber-shaped body, astromate, usually indehiscent, rarely opening by a pore. The spherical or pyriform asci bear from 2 to 8 spores which may be from 1 to many-celled. Conidia are produced in great abundance.

In *Aspergillus* and *Penicillium* fertilization is accomplished by conjugation of a straight oögonium with a spirally coiled antheridium, this act resulting in an ascogenous hypha. A reduced form of sexuality consisting of fusion of the nuclei of the ascogonium with each other probably also occurs.

KEY TO GENERA OF Aspergillaceæ

- | | |
|--|-------------------------------|
| Spores 1-celled, perithecium not beaked, unappendaged; peridium membranous or fleshy | |
| Conidia borne directly on the mycelium; chlamydospores borne in chains | 1. <i>Thielavia</i> , p. 123. |
| Conidia borne on distinct conidiophores in chains | |
| Conidiophores enlarged apically bearing numerous sterigmata | 2. <i>Aspergillus</i> p. 124. |
| Conidiophores bushy branched, single; perithecia sessile | 3. <i>Penicillium</i> p. 125. |

Thielavia Zopf

T. basicola (B. & Br.) Zopf

This, the one species of the genus, is on the boundary between the Aspergillales and the Perisporiales and is classed by some with the one, by some with the other order.

The ascocarps, which are the form less commonly seen, are

round, brown, completely closed and have no appendages. The asexual spores are of two kinds. First: hyaline conidia produced endogenously within "pistol-formed" conidiophores from the ends

of which they are expelled. Second: short cylindrical conidia or chlamydospores with a thick brown wall; borne in series of three to six on the ends of hyaline branches, Fig. 120. These conidia fall apart as they age.

The hyaline conidia preponderate in early disease, giving the surface of the root a mildewed appearance; the dark conidia preponderate later, covering the root with a black coating. Finally, after the host is dead, the ascocarps appear.

Very young seedlings may be killed. Older plants are invaded only in the roots, the root tissue being browned and killed.



FIG. 120.—*T. basicola*, showing two conidial forms and ascus and ascospores. After Van Hook and Zopf.

The delicate hyaline mycelium wanders through the affected root disorganizing its tissue. The superficial mycelium is lightly tinted.

Perithecia 80–100 μ ; asci ovate, 8-spored; spores lenticular, vacuolate, 1-celled, chocolate-colored, 8–12 x 4–5 μ ; chlamydospores in chains, at maturity separating, short-cylindric, about 5–8 x 12 μ ; the entire group 25–65 μ long; conidia hyaline, about 10–20 x 4–5 μ .

It primarily attacks legumes, cucurbits and the Solanaceæ, but is known in fifteen other families on nearly 100 hosts, among them *Aralia*, *Begonia*, *Catalpa*, *Cyclamen*, cotton, *Linaria*, *Lupinus*, *Nasturtium*, tobacco, bean, pea, sweet pea, clover, ginseng, cowpea, violet.

Aspergillus Micheli (p. 123)

The ascocarps are small, spherical, indehiscent, smooth bodies which at maturity are entirely filled with 8-spored asci; spores

1-celled. The conidiophores, which serve better to characterize the genus, are swollen at the end, and bear numerous sterigmata on which the spores are borne basipetally in chains. (See p. 380.)

Penicillium Link (p. 123)

The ascocarp is much as in the last genus, with the asci 4 to 8-spored. It may develop directly from the mycelium or with the intervention of a sclerotial stage. The characteristic conidiophore serves to distinguish the genus by its mode of branching. Fig. 347. Instead of being apically swollen as in the preceding genus it branches repeatedly, the branches bearing terminal sterigmata and giving the conidiophore the appearance of a brush; hence the name. For species see page 381.

Myriangiales¹ (p. 94)

Ascocarp stromatic, superficial, immersed or erumpent; asci irregularly disposed.

Plectodiscelleæ

Ascocarp innate, indefinite; stroma colorless, prosenchymatic, with a dark, clypeus-like cover.

Plectodiscella Woronin

Spores colorless, transversely 4-celled.

P. veneta Burk.

Ascocarp pulvinate, minute (75 μ), brown to black, scattered or grouped, stromatic. Asci globose, thick-walled, 24–30 μ in diameter, 8-spored, scattered irregularly in the stroma. Spores ovate, 4-celled, 18–21 x 6–8 μ , hyaline, constricted at the septa.

Conidial stage (=Gloeosporium venetum Speg.) caulicolous or foliicolous; spots orbicular or elliptic, border raised, darker, 2–3 mm. in diameter; conidia in acervuli on short, simple conidiophores, continuous, oblong, elliptic, 5–7 x 3 μ , in mass amber-colored.

The fungus occurs on all aerial parts of the raspberry causing serious disease. It was first reported in Italy in 1879. On canes small purple spots first show near the ground, enlarge and soon develop ashen centers. The leaf spots are small, often scarcely 1 mm. in diameter.

¹ Theissen and Sydow, Syn. Taf. 1. c.

The ascocarps appear in August and the asci mature, usually, in the following spring, the spores being liberated by disintegration of the overlying stromatic tissue. Hibernation is chiefly as



FIG. 121.—*P. veneta*, ascocarp showing arrangement of the asci in the stroma, After Burkholder.

mycelium within the canes. On canes infection results in death and collapse of the epidermal and cortical cells accompanied by hyperplasia of the parenchyma and phloëm. Abnormal growth tensions develop leading to fissures.

Myriangiaceæ

Perithecia erumpent, free, definitely formed. Stroma not slimy incrusted. Interascicular stroma cellular, not paraphysate; asci in several series.

Myriangium Mont. & Berk.

Ascigerous region locally limited from a sterile basal stroma, spores hyaline, muriform; no free mycelium. A species has been reported on the pecan.

Pyrenomycetes

The following five orders are usually grouped together as the Pyrenomycetes; separated from the preceding forms by their closed ascocarp with the asci arranged in a hymenium. They constitute a vast assemblage of more than ten thousand species, the large

majority saprophytic and unimportant except in the general economy as scavengers.

Perisporiales (p. 94)

The present order is characterized by its almost universally parasitic habit, the evident mycelium and the globoid perithecia without ostioles. The mycelium is superficial upon the host and frequently quite conspicuous.

KEY TO FAMILIES OF Perisporiales

- Mycelium white; perithecia with appendages.. 1. **Erysiphaceæ** p. 127.
 External mycelium dark colored or wanting
 Mycelium not slimy, straight-walled; perithecium not slimy..... 2. **Perisporiaceæ**, p. 142.
 Mycelium dematioid or straight-walled, but then slimy..... 3. **Capnodiaceæ**, p. 144.

Erysiphaceæ^{1,2,3}

This family on account of its abundance everywhere, its simplicity of structure, and its possession of typical ascigerous and conidial stages forms a favorite type for introductory study of the Ascomycetes. Its members are easy of recognition, forming a coating of white conidia, conidiophores and mycelium upon the surface of its hosts and giving them an appearance much as though they had been lightly dusted with flour. Later in the season the white patches are more or less liberally sprinkled with the black perithecia leading to the common name powdery mildew.

The mycelium except in *Phyllactinia* is entirely superficial. It is usually quite hyaline and is branched, septate and its cells uni-

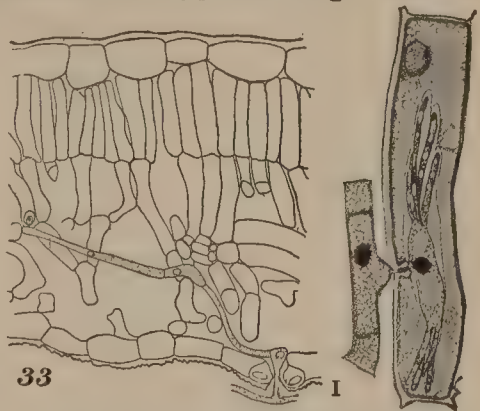


FIG. 122.—I, *E. graminis*, showing branching haustoria. 33, *Phyllactinia*, intercellular hyphae. After Smith.

¹ Salmon, E. S. Monograph of the Erysiphaceæ. Mem. Torr. Bot. Cl. 9: 1900.

² Halstead, B. D. N. J. Agr. Exp. Sta. Rept. 24: 517-536, 1903.

³ Reed, G. M. The powdery mildews. Erysiphaceæ. Trans. Amer. Micr. Soc. 32: 219, 1913.

nucleate. It fastens to the host and penetrates its epidermal cells by uninucleate haustoria which by their various lobings aid in specific characterization. Figs. 122, 123.

Haustroria may be grouped in three general classes; (1) those arising directly from the lower surface of the mycelium; (2) those arising at the side of the mycelium as small semicircular processes; (3) arising from more or less deeply-lobed lateral swellings of the mycelium.

The conidia arise in basipetal succession on simple, scattered conidiophores (Fig. 129); are hyaline, oval or barrel-shaped, smooth, 1-celled. They vary greatly in size with nutrition conditions.

Conidia germinate readily at once in dry air, better in humid air, producing from one to three germ tubes. Haustoria are formed at once and the mycelium develops to a more or less circular colony, producing new conidia in a few days. Artificial inoculations on susceptible plants, using conidia, usually result within two to five days in typical mildew spots.

Neger who studied the germination of conidia extensively has shown that light hastens the growth of the germ tubes, which in many cases are negatively phototropic. Contact stimulus leads to the growth of apressoria.



FIG. 123.—Erysiphe, showing lobed haustoria. After Salmon.

The perithecia are subspherical, often somewhat flattened, white to yellow when young, dark to black and reticulated when mature; are without ostiole but are provided with appendages of various types, Figs. 130, 131, 134,

which give main characters to mark the genera. The appendages serve by hygroscopic movements to aid in the distribution of the fungus. The ascospores become free after dissolution of the perithecium by weathering. The asci are either solitary or quite numerous within the perithecium and bear two to eight hyaline spores each.

The conidia are short-lived, summer spores. The perithecia mature more slowly and constitute the hibernating condition. In some instances the ascus-form is unknown; the fungus is then classified solely by its conidial stage and falls under the form genus *Oidium* (see p. 379).

In *Sphærotheca* an antheridial and an oögonial branch, each uninucleate, are developed, and cut off by septa. The oögonium

enlarges; the antheridium lengthens, its nucleus divides, and a septum is run in separating the stalk cell from the antheridium. The sperm nucleus enters the oögonium and fuses with the oögonial nucleus. Simultaneous with fertilization occurs, from the stalk cell of the oögonium, the development of a sterile system of enveloping threads which surround and protect the fertilized oögonium and eventually mature into the perithecial wall. The fertilized oögonium divides several times transversely producing a series of cells, one of which is binucleate. This binucleate cell after fusion of its nuclei develops into the one ascus, characteristic of the genus. The ascus nucleus by division gives rise to the spore nuclei and the spores are cut out of the periplasm by reflexion of the astral rays.

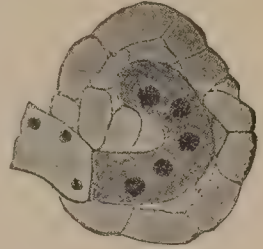


FIG. 124. — Ascogonium-tube with five nuclei. After Harper.

In *Erysiphe* the oögonium and antheridium arise in a very similar way, the oögonium being somewhat curved. Fertilization is also similar consisting of the union of two gametic nuclei. After fertilization the oöspore nucleus divides and the oögonium develops into a short bent tube, which contains from five to eight nuclei. Septa now appear cutting off cells, some uninucleate, some with two or more nuclei.

The ascogenous hyphæ develop a knot and soon divide into two or three cells each and give rise to the asci which are in the beginning binucleate.

In *Phyllactinia* the oögonium, antheridium and fertilizations are as in *Erysiphe*, though the oögonium may be quite curved so as to make almost a complete turn around the antheridium. Fig. 125.

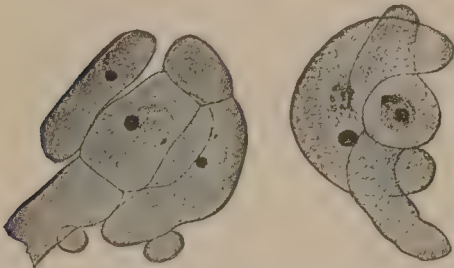


FIG. 125.—*Phyllactinia*, male and female branches; uninucleate oögonium and antheridium. After Harper.

After fertilization the antheridium degenerates and enveloping protective hyphæ arise both from the oögonium and the antheridium stalk cells. The oögonium becomes three to five nucleate and develops to a row of cells of which the penultimate cell has more than one nucleus. The ascigerous hyphæ arise from this binucleate cell, perhaps also from other cells of the series, become septate and form the asci either terminally, laterally or inter-

calary. The young ascus is binucleate, fusion follows and the spores develop as in the preceding genera.

The family contains, according to Salmon, forty-nine species and eleven varieties; according to Saccardo more than one hundred species. These are parasitic on some one thousand five hundred hosts, some of them upon economic plants and of marked harmfulness.

The matter of delimiting species and even genera is often difficult, owing to intergrading forms. This question is complicated still further by biologic specialization, such that forms, which are indistinguishable under the microscope, show in inoculation tests different abilities regarding host infection. Thus Neger, Salmon, Reed, and others have shown that spores borne on a particular host are capable of infecting only that host or in other cases only nearly related species of the same host genus. Forms which can pass from one genus to another are less common. Forms morphologically distinct are regarded as separate species. Differentiations within such species, regarding the species of host plant which they parasitize, give rise to "biologic species" or "biologic varieties."

Reed writes of these biologic forms thus:

"So far as investigated, *Erysiphe cichoracearum*, is the only one with doubtful exceptions, . . . shown to be capable of infecting plants belonging to more than one genus."

"There are other cases where the mildew is limited closely to plants of a single genus," and "Several cases are recorded where the mildew from one species will not infect other species of the same genus. Most of these claims, however, rest on insufficient data."

Some morphological species show a very wide range of hosts; one species, *Phyllactinia corylea* is known on forty-eight genera in twenty-seven families, others are limited to single genera or to single species of host plant. Two, three, and even five species are recorded for some species of host.

Geographically the Erysiphaceæ are widely distributed, practically of world distribution, but they are more abundant in the temperate zones than elsewhere.

A pycnidium-bearing parasite, *Cicinnobolus* is quite frequently found on the mycelium and conidiophores of the Erysiphaceæ.

Owing to the extreme variability of the perithecial characters this family presents a most difficult problem to the taxonomist who must either segregate or "lump" species. No middle ground seems open at present.

KEY TO SUBFAMILIES AND GENERA OF *Erysiphaceæ*

- Mycelium wholly external to the tissues of the host plant, usually sending haustoria into the epidermal cells only, perithecial appendages various, more or less flaccid
- I. *Erysipheæ*.
- Perithecial appendages indeterminate, similar to the mycelium, simple or irregularly branched
- Perithecia containing a single ascus . . . 1. *Sphærotheca*, p. 131.
- Perithecia containing several asci 2. *Erysiphe*, p. 133.
- Perithecial appendages determinate
- Appendages hooked or coiled at the apex 3. *Uncinula*, p. 136.
- Appendages dichotomous at the apex
- Perithecia containing a single ascus . . . 4. *Podosphæra*, p. 137.
- Perithecia containing several asci . . . 5. *Microsphæra*, p. 139.
- Mycelium with special intercellular haustoria-bearing branches which enter the host by the stomata; perithecial appendages rigid, with a bulbous base . . . II. *Phyllactinieæ*.
- A single genus 6. *Phyllactinia*, p. 141.

Sphærotheca, Léveillé

Perithecia subglobose; appendages floccose, brown or hyaline, spreading horizontally and often interwoven with the mycelium, simple or vaguely branched, frequently obsolete; ascus single, 8-spored. Five species, according to Salmon; Lindau gives fourteen.

S. humuli (DC.) Burr.

Amphigenous; mycelium usually evanescent; perithecia usually somewhat gregarious, but varying from scattered to cespitose, 58-120 μ in diameter; cells small, averaging 15 μ ; appendages few or numerous, usually long, often exceeding nine times the diameter of the perithecium, more or less straight, septate, dark brown throughout: variations are; short, flexuose, pearly-brown, white or even obsolete. Ascus broadly-elliptic to subglobose, rarely abruptly stalked, 45-90 x 50-72 μ ; spores 20-25 x 12-18 μ , rarely larger, averaging 22 x 15 μ .

Conidia (= *Oidium fragariæ*) ovate, white, membrane smooth.

Subjecting the conidia of this variety to low temperature, 0° two hours, increases their germinating power.

The species is cosmopolitan and among its numerous hosts are the economic genera *Dipsacus*, *Fragaria*, *Humulus*, *Phlox*, *Pyrus*, *Rosa*, *Ribes*, *Rubus*, *Scabiosa*, *Spirea* and *Viola*. A degree of host specialization exists.

It is a common rose mildew and is also destructive on the strawberry.

S. humuli* var. *fuliginea (Schl.) Salm.

Perithecia usually smaller than in the last, sometimes only $50\ \mu$ in diameter, wall usually harder and more brittle, cells larger, irregularly shaped, averaging $25\ \mu$; appendages usually short, pale brown; spores $20\text{--}25 \times 12\text{--}15\ \mu$.

It is recorded on *Arnica*, *Calendula*, *Coreopsis*, *Fragaria*, *Gailardia*, *Impatiens*, *Phlox*, *Scabiosa*, *Taraxacum*, *Verbena*, *Viola*.

S. pannosa (Wallr.) Lév.

Mycelium persistent, forming dense satiny patches on the stem, calyx, petiole, and rarely on leaves, at first shiny white, then becoming gray, buff or rarely brown; perithecia more or less,

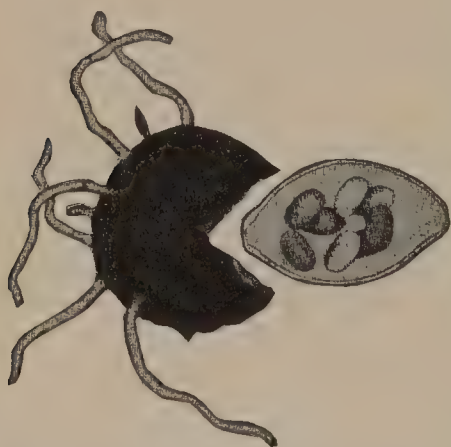


FIG. 126.—*S. mors-uvæ*, a perithecium discharging its single ascus which contains eight spores. After Longyear.

usually completely, immersed in the persistent mycelium, globose to pyriform, $85\text{--}120\ \mu$ in diameter, usually about $100\ \mu$, cells obscure, about $10\ \mu$ wide; appendages few, often obsolete, very short, tortuous, pale brown, septate; ascus broadly-oblong to globose, $88\text{--}115\ \mu$, averaging $100 \times 60\text{--}75\ \mu$; spores $20\text{--}27 \times 12\text{--}15\ \mu$.

Conidia (= *Oidium leucoconium*) ovoid, $20\text{--}30 \times 13\text{--}16\ \mu$, hyaline; conidiophores short.

Hosts: peach and rose.

The conidia are very common on the rose, but the perithecia are rare. What often passes for this species on roses in America is in reality *S. humili*.

S. mors-uvæ (Schw.) B. & C.

The mycelium at first white, is exceptional among the *Erysipheæ* in that it later becomes quite brown. It is found in closely felted patches on stems and fruit. Perithecia begin to form in June.

Amphigenous; mycelium persistent, at maturity forming dense pannose patches of brownish hyphæ; perithecia gregarious, more

or less immersed in the persistent mycelium, subglobose, 76–110 μ in diameter; cells large, at first well defined, then becoming obscure, 10–25 μ wide; appendages usually few or even obsolete, pale-brown, short, rarely longer, up to five times the diameter of the perithecium, tortuous; ascus elliptic-oblong to subglobose, 70–92, rarely 100 x 50–62 μ ; spores 20–25 x 12–15 μ .

On wild and cultivated species of *Ribes* in America; whence it was introduced into Europe where it is very destructive.

S. lanestris Hark. occurs on various species of oaks.

Erysiphe Hedwig (p. 131)

Perithecia globose, or slightly depressed, rarely concave; appendages floccose, simple or irregularly branched, sometimes obsolete, usually more or less similar to the mycelium and interwoven with it; asci several, 2 to 8-spored.

Salmon recognizes eight species; Lindau, twenty.

***E. polygoni* DC.**

Amphigenous; mycelium very variable, persistent, thin, effused and arachnoid, rarely thick, or more often evanescent; perithecia gregarious or scattered, usually rather small, averaging 90 μ , but ranging from 65 to 180 μ ; cells usually distinct, 10–15 μ wide; appendages very variable in number and length, few or many, distinct or more or less interwoven with the mycelium, brown or colorless; asci 2–8 or rarely as many as 22, variable in shape and size, usually small and ovate, with or without a short stalk, 46–72 x 30–45 μ ; spores 3–8 rarely 2, 19–25 x 9–14 μ .



FIG. 127.—*E. polygoni*, the asci. After Salmon.

Conidiophores (= *Oidium balsamii*).

Destructive to the pea and turnip. It was studied by Salmon on one hundred ninety host species belonging to eighty-nine genera; one hundred forty-six more hosts, some doubtful, are reported. Among the economic host genera are *Adonis*, *Alyssum*, *Anemone*, *Aquilegia*, *Brassica*, *Calendula*, *Catalpa*, *Clematis*, *Cucumis* (?), *Cucurbita* (?), *Dahlia*, *Daucus*, *Delphinium*, *Dier-villa*, *Dipsacus*, *Fagopyrum*, *Lupinus*, *Lycopersicum*, *Medicago*, *Pæonia*, *Phaseolus*, *Pisum*, *Tragopogon*, *Trifolium*, *Verbena*, *Vicia*, *Vigna* (cowpea) *Scabiosa*, *Symphytum*, *Valeriana*.

This is the most variable species of this genus, varying widely in its every character. It includes several species which have by

some been set aside as distinct, e. g., *E. martii*, *E. umbelliferarum* and *E. liriodendri*.

Salmon found that the conidia of this form grown on *Trifolium pratense* were unable to infect other species of *Trifolium*.

***E. cichoracearum* DC.**

Amphigenous; mycelium usually evanescent, rarely persistent, white or sometimes pink; perithecia gregarious or scattered, 80-140 or rarely 180 μ ; cells variable, often very distinct, 10-20 μ ; appendages variable in number and size, some shade of brown;

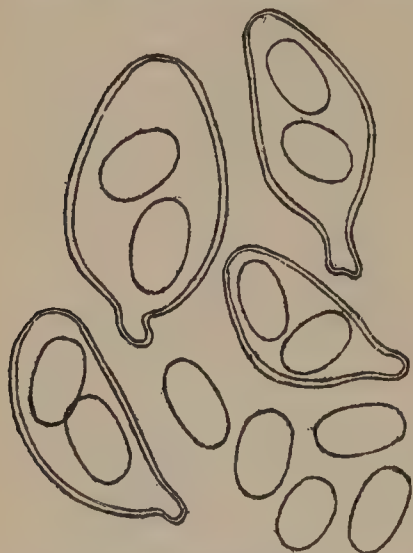


FIG. 128.—*E. cichoracearum*, asci and spores. After Salmon.

asci usually numerous, about 10-15, but varying from 4 to 36, variable in size and shape, narrowly ovate or subcylindric to broadly-ovate, more or less stalked, 58-90 x 30-35 μ ; spores 2, rarely 3, 20-28 x 12-20 μ .

Conidiophores (= *Oidium ambrosiæ* Thüm), short; conidia minute, elliptic, white, 4-5 x 2.5-3 μ . The species is quite variable, sometimes closely approaching *E. polygoni*.

The hosts are very numerous, among them being: *Calendula*, *Centaurea*, *Cichorium*, *Clematis*, *Cucurbita*, *Dahlia*, *Helianthus*, *Humulus*, *Mentha*, *Nicotiana*,

Phlox, *Tragopogon*, *Valeriana*, *Verbena*, *Symphytum*. It is of especial import on composites and cucurbits.

Reed has made very extensive culture studies of this species and concludes that the same form of "*Erysiphe cichoracearum* DC.", occurs on at least eleven species of the cucurbits, belonging to seven genera, infection occurring in these cases in fifty per cent or more of the trials. Six other species were also infected, but in a smaller percentage of cases. . . . It is also plain that the biologic form of *Erysiphe cichoracearum*, occurring on so many cucurbits is not entirely confined to the species of this one family. Out of fifty-four leaves of *Plantago rugelii*, a species belonging to the Plantaginaceæ, which were inoculated, ten became infected. . . . Furthermore out of ten leaves of squash seedlings, inoculated with conidia from plantain, six became infected . . . and the sunflower,

Helianthus annuus, was infected in thirty-five per cent of the trials in which conidia from the squash were sown on leaves of seedlings. . . . The cucurbit mildew could not be transferred to asters and goldenrods nor was the mildew occurring on these in nature able to infect the squash. Neither the aster mildew nor the cucurbit mildew proved able to infect a goldenrod, *Solidago cæsia*. Nor was the mildew on this host able to infect asters or squashes."

***E. graminis* DC.**

Usually epiphyllous, rarely amphigenous; mycelium more or less persistent, forming scattered patches, at first white, then brown or gray; perithecia large, 135–280 μ , usually about 200 μ , scattered or gregarious, cells obscure; appendages rudimentary, few or numerous, very short, pale brown; asci numerous, 9–30, cylindric to ovate-oblong, more or less long-pedicellate, 70–108 x 25–40 μ ; spores 8, rarely 4, 20–23 x 10–13 μ , seldom produced on the living plant.

Conidial form (= *Oidium monilioides*) with a grayish cast; conidiophores medium tall; conidia ovoid, white or sordid, 25–30 x 8–10 μ .

It is found on a large number of species of the Gramineæ including species of *Avena*, *Festuca*, *Hordeum*, *Phleum*, *Poa*, *Saccharum*, *Secale*, and *Triticum*.

The asci are peculiar in that they usually contain undifferentiated granular protoplasm, not spores, though in some cases the spores, normally 8, are present.

This species on grasses shows no morphological differences, yet inoculation tests have revealed in it numerous biologic varieties. Reed summarizes the results of his own work together with that of Marchal and Salmon as follows:

"So far as tested, all species of *Avena* are susceptible to the oat mildew. All species of *Triticum* are likewise susceptible to the wheat mildew. We find, however, that certain varieties of *Triticum dicoccum* are practically immune to the wheat mildew. Other varieties of this same species are entirely susceptible. Some species of *Hordeum* are immune to the barley mildews, and the same seems to



FIG. 129.—*E. graminis*, conidial stage. After Salmon.

be true of certain species of *Secale* with reference to the rye mildew.

"To these general statements there are two possible exceptions. Marchal states that the oat mildew will infect *Arrhenatherum elatius*. Salmon, however, obtained a negative result with the oat mildew on this grass. The evidence is not conclusive either way. The other exception is that, according to Salmon, conidia from wheat can infect *Hordeum silvaticum*.

"It would seem then that under normal conditions there are well-defined forms of *Erysiphe graminis* occurring respectively on the species of each of the four cereals."

It is thought that some hosts may act as bridging species and enable the parasite to pass from one host to another to which it could not pass directly.

***Uncinula* Lévillé (p. 131)**

Perithecia globose to globose-depressed; appendages simple or rarely once or twice dichotomously forked, uncinatate at the apex, usually colorless, rarely dark brown at base or throughout; asci several, 2 to 8-spored.

There are eighteen or twenty species.

***U. necator* (Schw.) Burr.**

Amphigenous; mycelium subpersistent; perithecia usually epiphyllous, occasionally hypophyllous or on the inflorescence, more or less scattered, 70–128 μ ; cells distinct, rather irregular in shape, 10–20 μ ; appendages very variable in number and length, 7–32, rarely up to 40, 1 to 4-times the diameter of the perithecium, septate, thin walled, light or dark amber-brown basally, rarely branched, asci 4–6 rarely up to 9, broadly-ovate or ovate-oblong to subglobose, with or without a short stalk, 50–60 x 30–40 μ ; spores 4–7, 18–25 x 10–12 μ .

Conidial form (= *Oidium tuckeri*), conidiophores short; conidia elliptic, oblong, or obtusely rounded, 2 to 3-catenulate, hyaline, 25–30 x 15–17 μ .

Hosts: *Vitis*, *Ampelopsis* and *Actinidia*. This species is one of the worst pests of the family.

The mycelium is thin walled and sparingly septate. The haustoria arise from lobed lateral swellings of the hyphae, penetrate the epidermis with a filamentous projection and swell within the host cell to a bladder-like body. The parasitized cells and later the neighboring ones turn brown and die.

The conidia germinate readily in moist air or in water, sending forth from one to several germ tubes.

The perithecia are found well developed as early as June or July in the United States and are rather evenly scattered over the affected surfaces. A period of warm moist weather which favors luxuriant mycelial growth, followed by sudden lowering of temperature to about 50° F., favors their most rapid formation. They are at first hyaline, later brown. After their form and walls become definite, usually during winter, the appendages develop as outgrowths from the outer walls. During winter the appendages break off. Galloway failed to secure germination of ascospores earlier than February or March, but perithecia which had been exposed to the weather until spring and were then placed in a hanging drop culture afforded spores, some of which grew though many of them burst as they emerged from the perithecium. Ascospores are known to have remained viable for at least eighteen months. No successful infections were made from ascospores.

Though perithecia are frequently found in America they were not found in Europe until 1892 and are now found there but rarely. It appears that in their absence the fungus hibernates in specially resistant cells of the mycelium which develop within knotty swellings near the haustoria.

Other species are *U. salicis* (DC.) Wint. on willow and poplar, *U. aceris* (DC). Sacc. and *U. circinata* C. & P. on maple, *U. flexuosa* Pk. on *Æsculus*, and elm, *U. clandestina* (Biv.) Schr. on elm, *U. prunastri* (DC.) Sacc. on *Prunus*.

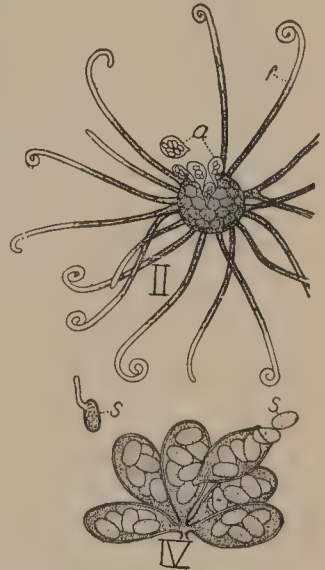


FIG. 130.—*U. necator*. II. Perithecium showing *f*, appendages, and *a*, asci. IV. Group of asci removed from perithecium emitting *s*, ascospores. After Viall.

Podosphæra Kunze (p. 131)

Perithecia globose or globose-depressed; ascus solitary, subglobose, 8-spored; appendages equatorial or apical, dark-brown or colorless, dichotomously branched at the apex, branches simple and straight or swollen and knob-shaped; appendages rarely of

two kinds, one set apical, brown, rigid, unbranched or rarely 1 to 2-times dichotomous at the apex, the other set basal, short, flexuous, frequently obsolete.

Salmon recognizes four species; Lindau seven.

P. oxyacanthæ (DC.) de Bary

Amphigenous; mycelium variable, persistent in thin patches or evanescent; perithecia scattered or more or less gregarious, subglobose, 64–90 μ ; cells 10–18 μ ; appendages spreading more or less, equatorial, variable in number and length, from 4–30 in number and from $\frac{1}{2}$ –6 or even 10-times the diameter of the perithecium, usually unequal in length, dark brown for more than half their length from the base, apex 2 to 4-times dichotomously branched, branches usually short and equal, ultimate branches rounded, swollen, and more or less knob-shaped, Fig. 131, ascus broadly obovate, or subglobose, 58–90 x 45–75 μ ; spores 8, rarely 6, 18–30 x 10–17 μ .



FIG. 131.—*P. oxyacanthæ*, appendage tips. After Salmon.

Conidia (= *Oidium cratægi*).

On some hosts perithecia are rare. It is thought that the mycelium remains alive over winter.

Hosts: *Amelanchier*, *Cratægus*, *Diospyros*, *Prunus*, *Pyrus*, *Spirea* and *Vaccinium*. Especially damaging to cherry and apple. Throughout the northern hemisphere.

P. tridactyla (Wallr.) de Bary is considered by Salmon as a variety of the last species. Hosts: Plum and other species of *Prunus* and of *Spirea*.

Similar to the preceding in habit and general character but differing in more critical characters. Perithecia 70–105 μ ; cells 10–15 μ ; appendages 2–8 usually 4, 1 to 8-times the diameter of the perithecium, apical in origin, more or less erect, apically 3–5 or 6-times dichotomously branched, primary branches usually more or less elongate, sometimes slightly recurved; asci globose or subglobose, 60–78 x 60–70 μ ; spores 8, 20–30 x 13–15 μ .

P. leucotricha (E. & E.) Salm.

Mycelium amphigenous, persistent, thin, effused; perithecia densely gregarious, rarely more or less scattered, 75–96 μ , subglobose, cells 10–16 μ ; appendages of two kinds, one set apical the other basal; apical appendages 3–11 in number, more or less widely spreading, or erect-fasciculate, 4 to 7-times the diameter of the perithecium, apex undivided and blunt or rarely once or

twice dichotomously branched, brown basally; basal appendages nearly obsolete or well developed, short, tortuous, pale brown, simple or irregularly branched; ascus oblong to subglobose, $55-70 \times 44-50 \mu$, spores $22-26 \times 12-14 \mu$, crowded in the ascus.

Conidia (=Oidium farinosum): ellipsoid, truncate, hyaline, $28-30 \times 12 \mu$.

This and *P. oxyacanthæ*, the apple mildews of America, have been variously treated by writers so that the literature presents an almost inextricable tangle, *Podosphæra oxyacanthæ* being frequently reported instead of *P. leucotricha*. *Sphærotheca mali* and *Podosphæra oxyacanthæ* have also been much confused, due to similarity of habit and the frequent abnormal development of the appendages, so that the published references are not always reliable.

Though invasion is only into the epidermis by haustoria the infected leaves are stunted, the internodes shortened; also twigs may be thickened. It has been demonstrated that the mycelium passes the winter in a dormant condition within buds and as these open in the spring growth resumes.

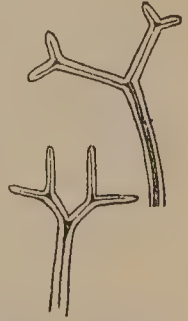


FIG. 132.—*P. leucotricha*, appendage tips. After Salmon.

Microsphæra Léviellé (p. 131)

Perithecia globose to subglobose; asci several, 2 to 8-spored appendages not interwoven with the mycelium, branched in a definite manner at the apex, usually dichotomously and often very ornately, rarely undivided or merely once dichotomous.



FIG. 133.—*M. grossulariæ* appendage tips. After Salmon.

According to Salmon there are thirteen species; Lindau recognizes thirty.

M. grossulariæ (Wallr.) Salmon

Epiphyllous or amphigenous; mycelium evanescent or subsistent; perithecia scattered or densely aggregated, globose-depressed, $65-130 \mu$; cells $14-20 \mu$; appendages $5-22$, colorless, $1-1\frac{3}{4}$ times the diameter of the perithecium, 4 to 5-times closely dichotomously branched, branches of first and second order very short, all segments deeply divided, tips not recurved; asci 4-10,

broadly ovate or oblong, usually with a very short stalk, 46–62 x 28–38 μ ; spores 4–6, rarely 3, 20–28 x 12–16 μ .

On five species of *Ribes* and two of *Sambucus*. This is the European gooseberry-mildew, common on America only on the elder.

M. alni (Wallr.) Lév.

Amphigenous; mycelium evanescent or persistent; perithecia scattered to gregarious, globose-depressed, very variable in size, usually small, 66–110 μ , or even up to 135 μ ; cells 10–15 μ wide; appendages variable in number (4–26) and length, $\frac{1}{3}$ to $2\frac{1}{2}$ times the diameter of the perithecium, more or less rigid, colorless throughout or amber-brown at base, apex variously, but not always, more or less closely 3 to 6-times dichotomously branched, tips of ultimate branches regularly and distinctly recurved; asci 3–8, ovate to ovate-globose, 42–70 x 32–50 μ , usually but not always short stalked; 4 to 8-spored; spores 18–23 x 10–12 μ .



FIG. 134.—*M. alni*, appendage tips.
After Salmon.

This species is the most variable of the *Erysipheæ* showing large latitude in number of spores in the ascus, in length, color and branching of appendages, in size of perithecia. It occurs upon very

numerous hosts. The economic ones on which it is most common are: *Syringa*, *Lonicera*, *Alnus*, *Betula*, *Quercus*, *Carya*, *Pecan*, *Castanea*, *Juglans*, *Platanus*, Sweet pea.

It is confined to the northern hemisphere.

Salmon recognizes in addition to the typical form six varieties.

M. diffusa C. & P.

Amphigenous; mycelium persistent, thin and effused, or sub-persistent and forming vague patches, or quite evanescent; perithecia scattered or gregarious, globose-depressed, very variable in size, 55–126 μ in diameter, averaging 90–100 μ , cells 10–20 μ wide; appendages very variable in number and length, 4–30, or rarely crowded and as many as 50, $1\frac{1}{2}$ to 7-times the diameter of the perithecium, smooth, aseptate or 1 to 3-septate in the lower half, colorless or pale brown towards the base, flaccid when long, thin-walled above, becoming thick-walled towards the base, apex 3 to 5-times dichotomously or subdichotomously divided, branching diffuse and irregular, branches of the higher orders sub-nod-

ulose, often apparently lateral, tips of ultimate branches not recurved; asci 4-9, 48-60 x 28-30 μ , ovate-oblong with a very short stalk; spores 3-6, usually 4, 18-22 x 9-11 μ .

Hosts; *Desmodium*, *Glycyrrhiza*, *Lespedeza*, *Phaseolus*, *Symphoricarpus*.

M. euphorbiæ (Pk.) B. & C. occurs on various hosts including *Astragalus*, *Colutea*, *Cuphea* and *Euphorbia*. Its only economic importance is as the cause of a disease of the roselle and cowpea on which it is very common.

Amphigenous; mycelium usually subgeniculate; perithecia gregarious in floccose patches or scattered, 85-145 μ , rarely 180 μ , cells 10-15 μ ; appendages 7-28, usually narrow, more or less flexuose and nodose, 2.5 to 8-times the diameter of the perithecium, colorless above, 3 to 4-times dichotomously branched, branching, irregular and lax, asci 4-13, rarely up to 26, ovate or ovate-oblong, short-stalked, 48-66 x 26-35 μ ; spores usually 4, rarely 3, 5 or 6, 16-21 x 10-12 μ .

Phyllactinia L  veill   (p. 131)

Perithecia large, globose-depressed to lenticular; asci many, 2 or 3-spored; appendages equatorial, rigid, acicular, with a bulbous base; apex of perithecium with a mass of densely crowded branched outgrowths.

Typical epidermal haustoria are not produced but the mycelium sends special branches through the stomata into the intercellular spaces of the leaf. These branches attain some length and constitute a limited internal mycelium, a character that is considered by some as of sufficient importance to set the genus apart in a separate family. The internal mycelium gives off haustoria which penetrate cells of the mesophyll. The appendages exhibit striking hygroscopic movements and aid in dissemination.

Only one species is recognized by Salmon.

P. corylea (Pers.) Karst.

Hypophyllous or rarely amphigenous; mycelium evanescent or more or less persistent; perithecia usually scattered, rarely gregarious, 140-270 μ , rarely up to 350 μ ; cells rather obscure, 15-20 μ ; the apical outgrowth becomes mucilaginous attaching the perithecium firmly to places where it may fall; appendages 5-18, equatorial, 1 to 3-times the diameter of the perithecium; asci 5-45, subcylindric to ovate-oblong, 60-105 x 25-40 μ , more or less stalked, 2, rarely 3-spored; spores 30-42 x 16-25 μ .

Conidia (=Ovulariopsis), acrogenous, solitary, hyaline, subclavate.

On Magnolia, Liriodendron, Berberis, Xanthoxylum, Ilex, Celastrus, Acer, Desmodium, Cratægus, Heuchera, Ribes, Hamamelis,

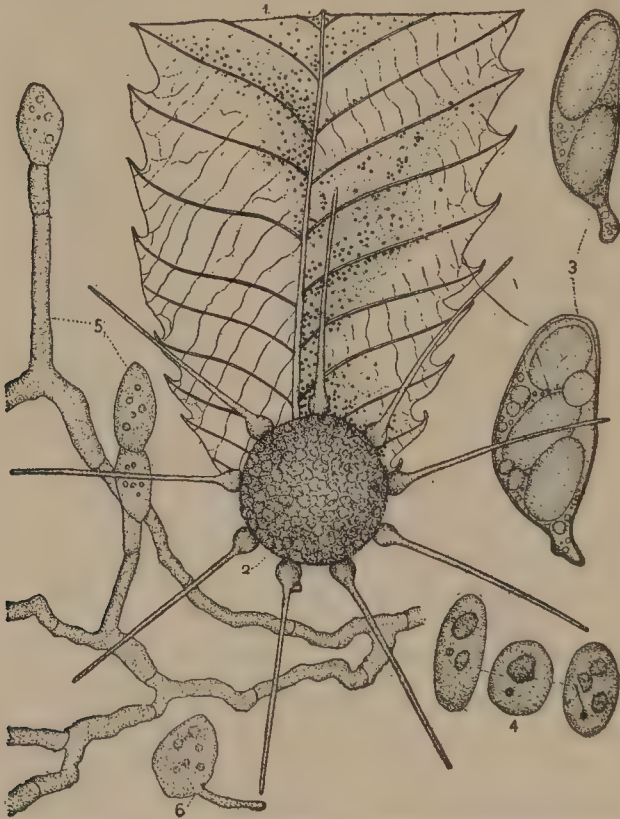


FIG. 135.—*Phyllactinia corylea*. 1. Natural size, on chestnut leaf. 2. Perithecium enlarged. 3. Two asci. 4. Three spores. 5. Conidia-bearing hyphæ. 6. Conidium germinating. After Anderson.

Fraxinus, *Asclepias*, *Catalpa*, *Cornus*, *Ulmus*, *Betula*, *Alnus*, *Corylus*, *Ostrya*, *Carpinus*, *Quercus*, *Castanea*, *Fagus*, and *Typha*.

Perisporiaceæ (p. 127)

Mycelium mostly superficial, dark, not dematioid, no typical ostiole.

Cleistothecopsis Stevens & True

C. circinans. Stevens & True

Perithecia superficial, irregularly globular, 89.6–313.6 μ in di-

ameter, dark brown to black, no ostiole, surface reticulate, often with numerous short hairs extending out from surface cells, entirely pseudoparenchymatous, outer layer of darker, thick-walled cells; asci clavate, basal, evanescent, 8-spored, approximately $72-96 \times 19-24 \mu$; paraphyses present but evanescent; ascospores

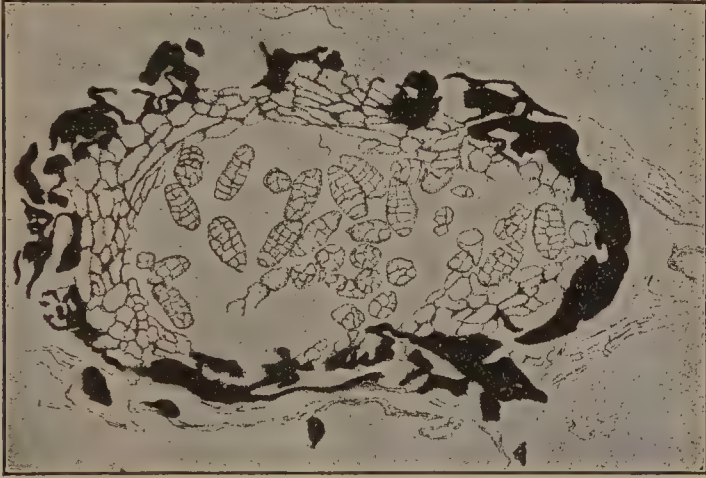


FIG. 136.—A peritheciium of *Celistothecopsis* with mature free spores. After Stevens and True.

muriform, dark, obtuse at each end, usually with 4–7 transverse and 1–2 longitudinal septa, $24-36 \times 9.6-14.4 \mu$.

Its conidial form is *Volutella circinans*. Sporodochia scattered or often in concentric circles, usually in the centers of infected areas, numerous, black, subepidermal, erumpent, becoming covered with loose mycelium, 1–2 mm. in diameter, 1 mm. in elevation. Mycelium hyaline, becoming dark, rather coarse, $3.6-10.8 \mu$ wide, branching irregularly, and with characteristic darkening of end cells where mycelium is superficial. Setæ one to many, scattered throughout, dark brown to black, $125-240 \mu$ long, 4μ wide at base, tapering to apex. Conidiophores straight, simple, hyaline, few-septate, obtuse, $24-48 \times 2.4 \mu$, bearing conidia acrogenously. Conidia falcate, acute at each end, continuous, hyaline, $19-26 \times 3.6-7.2 \mu$.

On onions, developing particularly during storage. The dark coarse, septate mycelium forms dense mats within the onion tissue, either inter- or intracellular or even superficial. Under suitable conditions a sporodochium, which has been described both as

a pycnidium and as an acervulus develops and bears the spores. Perithecia are but rarely seen.

Capnodiaceæ (p. 127)

Fungus superficial. Mycelium dematium-like or if straight-walled, slimy: hyphopodia rare.

This family constituting the "sooty molds"¹ consists of numerous genera. They, so far as is known, do not penetrate the host at all and probably, strictly speaking, do not cause disease. They are especially abundant in the tropics and sub-tropics and are injurious in that they disfigure leaves or fruit. Those on the orange and camellia are of most importance.

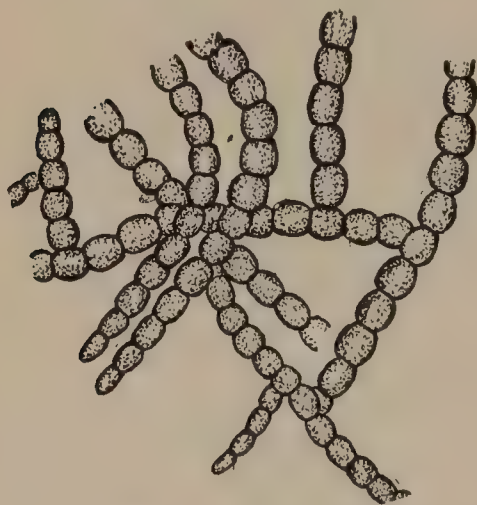


FIG. 137.—Beaded mycelium of the sooty mold.
After Mendoza.

Frequently, especially in extra tropical regions, the mycelium only is present, usually consisting of characteristic, beaded cells, Fig. 137, which was once given the form genus name *Fumago*. Under favorable conditions perithecia and pycnidia also develop, both of these being variable in character thus rendering exceedingly difficult the taxonomy of this group. The mycelium alone is quite inadequate for classification and, in the absence of perithecia, no classification is

possible. These uncertainties have led to much confusion. Thus the form on Citrus has been variously placed in the genera *Fumago*, *Capnodium*, *Meliola*, *Morfea* and *Limacinia*; and even regarded as consisting of three species bearing for example the names *Limacinia citri*, *L. penzigi*, *L. camelliæ*. All of these Arnaud unites under the name *Pleosphæria citri* Arn.

¹ Arnaud, G. Contribution à l'étude des Fumagines Ann. d. l'école nationale d'agriculture de Montpellier, **10**: 211, 1910-11; **12**: 23, 1912.

Hemisphæriales¹ (p. 95)

Perithecia dimidiate, superficial or subcuticular.

Microthyriaceæ

Mycelium superficial, dark, filamentous or lacking, perithecia superficial, shield-shaped, black, radiate, Asci 4 to 8-spored; short, paraphyses usually present.

Glæodes (see p. 360) probably is an imperfect form of some member of this order.

Diplocarpon Wolf

D. rosæ Wolf. (= *Actinonema rosæ*)

The vegetative body of the fungus consists of two parts, the subcuticular mycelium, made up of a net-work of branched radiating strands, and the internal mycelium which furnishes nutriment for the subcuticular part and is connected with it by hyphæ which penetrate the epidermal cells or pass between them. Single fila-

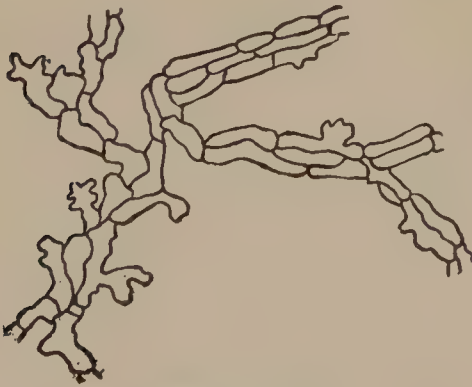


FIG. 138.—*D. rosæ* rhizomorph-like strands of mycelium. After Wolf.

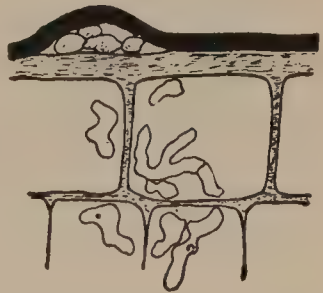


FIG. 139.—Vertical section showing the mycelium of *D. rosæ* under the cuticle and also within the epidermis and mesophyll. After Wolf.

ments are often more or less coralloid in appearance. At certain definite points on the mycelium a stroma begins to form, seated directly upon the epidermal cells. From these arise the conidia or summer spores, which soon become divided by a cross wall. In the following spring perithecia develop on the overwintered leaves.

¹ Theissen, F., and Sydow, H. Synoptische Tafeln. Ann. Myc. **15**: 396, 1917.

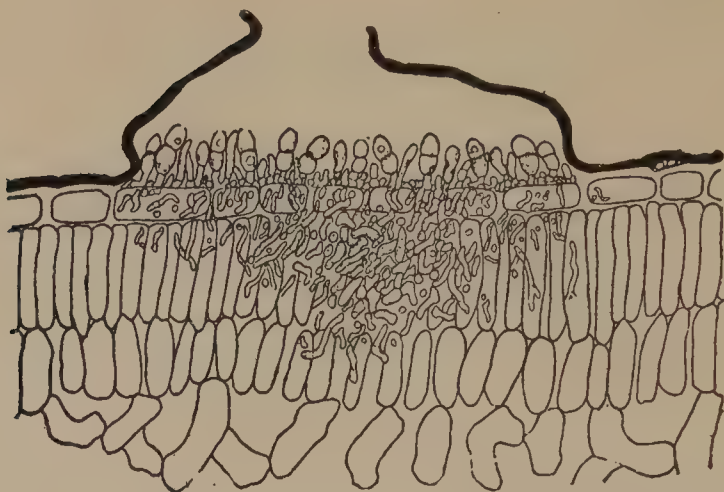


FIG. 140.—*D. rosae* vertical section through an acervulus. After Wolf.

Perithecia epiphyllous, spherical to disciform, 100–250 μ in diameter, radiate; asci 70–80 x 15 μ , 8-spored; spores 20–25 x 5–6 μ , unequally, 2-celled, hyaline. Conidia in an acervulus, 18–25 x 5–6 μ . Parasitic on rose leaves.

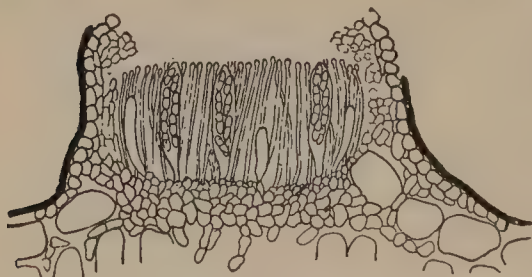


FIG. 141.—*D. rosae* vertical section through a mature perithecium. After Wolf.

Hypocreales^{1, 2} (p. 95)

The chief character separating this order from other Pyrenomycetes is the brighter color—yellow, purple, scarlet, red,

etc.—and the more tender texture of its perithecia,—soft, fleshy, cottony, patellate or effused.

The perithecium also differs from that of the preceding orders, excepting the last, in the possession of a distinct opening, ostiole, for the exit of spores.

Perithecia globose to cylindric or flask-shaped, free on the substratum, rarely subepidermal, or united by a common matrix, which varies from a cottony subiculum to a distinct fleshy stroma, wall membranous or at least not truly carbonous; asci cylindric,

¹ Seaver, F. J. Hypocreales. North American Fungi. **3**: 1, 1910.

² Seaver, F. J. Some North Dakota Hypocreales. Bull. Torr. Bot. Club. **35**: 527.

clavate or subovoid, mostly 4 to 8-spored but often becoming 16-spored by the separation of each original spore into two globose or subglobose cells; spores simple or compound, hyaline or colored, globose to filiform.

Conidia are usually produced freely, each genus usually possessing at least one form of free-borne conidia, while in some genera several different kinds of conidia are found. Pycnidia are rare. Often the ascigerous stage is nearly suppressed and rare when one or more of the conidial forms predominates.

Such form genera as *Fusarium*, *Verticillium*, *Tubercularia*, *Sphacelia*, *Sphaerostilbe* and *Isaria* are connected with the Hypocreales.

The order includes over sixty genera and more than eight hundred species. Of these few genera contain important plant parasites. The rest are saprophytes, insect parasites, etc., of little or no economic significance.

Only seven genera will be considered and they may be classified by the following key.

KEY TO GENERA OF Hypocreales

- | | |
|---|------------------------------------|
| Spores 2-celled | |
| Stroma cottony..... | 1. <i>Hypomyces</i> , p. 147. |
| Stroma not cottony | |
| Spores hyaline..... | 2. <i>Nectria</i> , p. 148. |
| Spores brown..... | 3. <i>Neocosmospora</i> . |
| Spores 1-many celled | |
| Perithecium not blue..... | 4. <i>Calonectria</i> , p. 150. |
| Perithecium blue..... | 5. <i>Gibberella</i> , p. 150. |
| Spores filiform | |
| Asci preceded by conidia..... | 6. <i>Claviceps</i> , p. 151. |
| Asci preceded by smut-like chlamydo-spores..... | 7. <i>Ustilaginoidea</i> , p. 153. |

Hypomyces (Fries) Tul.

Stroma an effused cottony subiculum, often of considerable extent; perithecia numerous, usually thickly scattered and immersed in the subiculum, rarely superficial; asci cylindric, 8-spored; spores fusoid or fusiform, usually apiculate, rarely blunt, 2-celled, hyaline; conidial phase variable.

This genus contains but few saprophytes, the majority being parasitic, chiefly on the larger fungi. Chlamydospores and conid-



FIG. 142.—*Hypomyces ochraceus*. B, perithecia; C, asci and spores; D, spores; E, conidia; F, chlamydospores. After Tulasne.

iospores develop, belonging to various form genera as *Verticillium*, *Mycogone*, *Fuligo*, *Diplocladium*, *Dactylium*, *Sepedonium*, *Blastotrichum*.

Allied to this genus are probably *Mycogone rosea* and *M. pernicios*, which are destructive enemies of mushroom culture. (See p. 393.)

Nectria Fries (p. 147)

Stroma absent or tubercular, fleshy, bright colored; perithecia single or gregarious, on or in the stroma or among cottony

hyphæ, globose or ovate, walls fleshy, yellow, red or brown, smooth or hairy; ostiole papillate or not; asci cylindric or clavate, 8-spored; spores elongate, blunt or pointed, hyaline, rarely red, 2-celled, forming conidia in the ascus; paraphyses usually none.

As conidial stages occur the form genera *Cephalosporium*, *Tubercularia*, *Fusarium*, *Spicaria*, *Fusidium* and *Chætostroma*. Much doubt exists as to specific limitations, and as to the life histories of the species. Several are credited with causing serious diseases, most of them occurring as wound parasites and unable to effect entrance into sound tissue. Other species are saprophytes and harmless.

N. cinnabarina (Tode) Fr.

Stroma erumpent, tubercular, at first pinkish or yellowish-red, darker with age, 1–2 mm. high and broad; perithecia almost globose, the ostiole rather prominent, becoming slightly collapsed, at first bright cinnabar-red, darker with age, granular, 375–400 μ in diameter; asci clavate, 50–90 x 7–12 μ ; spores mostly 2-seriate, elliptic elongate, ends obtuse, slightly curved, 12–20 x 4–6 μ ; paraphyses delicate.

Tubercularia vulgaris borne on the stroma is the conidial stage. Conidiophores aggregated into tubercular masses each 50–100 μ

long; conidia on short lateral branches, elliptic, hyaline, $4-6 \times 2 \mu$, no chlamydospores.

The closely septate delicate hyphæ grow rapidly through the wood or bark, penetrating nearly every cell, turning the wood black and collecting to form stromata on or in the bark. These stromata in fall or spring break through the epidermis and produce warty, gray to pink, excrescences, which at first bear profuse conidia both terminally and laterally on short stalks and later dark-red ascigerous structures; though the latter are much less common. The fungus is said to be unable to affect living cambium and cortex.

It is found saprophytically on many decayed woody plants that have been frost killed, and parasitically on pear, currant, linden, horse chestnut, Chinaberry, birch, elm, *Carya*, *Prunus*, maple, mulberry, oak, etc. Mayer germinated spores on a cut branch; the mycelium spread to and killed the main stem; tubercles appeared and during the following year perithecia developed on these tubercles.



FIG. 143.—*N. cinnabarina*, perithecia in stroma, ascospores issuing in cirri; germinating spores. After Hartig.

***N. galligena* Bres.=*Fusarium willkommii* Lind.**

Perithecia red, ovoid, $400-450 \times 275-325 \mu$; ascospores ovoid, 1-septate, $14-16 \times 5-7.25 \mu$; conidia cylindrical, mostly 5-septate, $57-73 \times 4.75-6 \mu$, but 30% of all conidia may be 6-septate, with average length up to 82μ . No true chlamydospores are present.

A wound parasite, cause of canker on apple trees and associated with canker on various other trees. This fungus is often confused with *Nectria ditissima* Tul., a probable saprophyte, which has shorter ascospores, $12-14 \mu$ long.

***N. cucurbitula* Sacc.**

Perithecial clusters erumpent, often irregular in form, 1-2 mm. in diameter; perithecia densely clustered, bright red, ovate, with a prominent ostiole, rarely collapsing; asci cylindric to clavate, $75-100 \times 6-8 \mu$; spores at first crowded and partially 2-seriate, finally becoming 1-seriate, lying obliquely in the ascus, broad, fusoid, rarely subelliptic, $14-16 \times 5-7 \mu$.

Its hosts are spruce fir, pine, and other conifers.

The fungus is usually a wound parasite, often following hail.

Germ tubes from ascospores or conidia enter the cortex and develop a rich mycelium in the sieve tubes and soft bast. This advances most rapidly during the dormant period of the bast.

White or yellow stromata the size of a pinhead appear and bear numerous conidia. Later come the red perithecia whose ascospores ripen in winter or spring.

Other species are on cherry, alder, arbor-vitæ, ash, beech, birch, box elder, Chinaberry, dogwood, elm, fir, hazel, *Æsculus*, linden, maple, mulberry, oak, pine, spruce, walnut.

***Calonectria* De Not.^{1, 2} (p. 147)**

Perithecia free, often closely gregarious, true stroma wanting but perithecia often surrounded by a radiate, white mycelium which may simulate a stroma; perithecia globose to ovate, red or yellow; asci elongate, 8-spored; spores elongate, more than 2-celled.

C. graminicola (Berk. & Br.) Woll. = *Nectria graminicola* Berk. & B. Perithecia brown, average diameter 125–200 μ (limits 75–300 μ); ascospores fusoid, 1 to 3-septate, 12–15 x 2.75–3.75 μ . Conidia (*Fusarium*) ochreous to salmon-colored, 3-septate, 23–26 x 3.25–4 μ , formed as a slightly curved comma. Instead of true chlamydospores a plectenchyma is present.

Cause of seedling blight, snow mould disease, on cereals.

***Gibberella* Saccardo (p. 147)**

Stromata tuberculate, more or less effused; perithecia cespitose or occasionally scattered on or surrounding the stroma; asci clavate, 8-spored; spores fusoid, 4 to many-celled, hyaline; conidial phase a *Fusarium*.

G. saubinetii (Mont.) Sacc.³ Perithecia blue, 150–250 x 100–250 μ , scattered, papillate, free on the surface of the host or embedded in mycelium or on a stroma. Asci 60–76 x 10–12 μ . As-

¹ Weese, J. Beitrage zur Kenntnis der Gattung *Calonectria*. Myc. Cent. **4**: 121, 1914.

² Wollenweber, H. W. Studies on the *Fusarium* problem. Phytop. **3**: 24, 1913.

³ Atanasoff, D. *Fusarium*-blight (scab) of wheat and other cereals. Jour. Agr. Res. **20**: 1, 1920.

cospores sickle-shaped, 3-septate, $20-30 \times 3.75-4 \mu$. Conidia similar to those of the section discolor of the genus *Fusarium*, 3 to 5-septate, $30-60 \times 4.25-5.5 \mu$. No true chlamydospores are present.

The cause of kernel scab and seedling blight, foot disease, on cereals especially wheat, emmer, rye, oats, spelt, and corn, also on clover.

On the roots and bases of young small grains enumerated above the fungus causes rot followed by wilting; on the nodes or heads blighting results.

The mycelium and the conidial stages often coat the grains and heads of cereals with red or pink. Perithecia are less common as shining dark dots on the grains in the late season. The *Fusarium* stage is also the cause of a clover and alfalfa disease and the fungus by inoculation and culture is shown to be identical on wheat, clover, barley, rye, spelt, emmer, oat and some other grasses. It is carried from season to season on infected seed and causes large loss of young plants. It survives the winter also in perithecia. Root infection follows in about seven days after inoculation: head infection in 3-6 days.

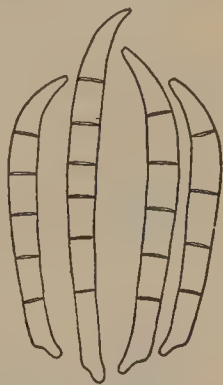


FIG. 144.—Conidia of *G. saubinetii*. After Atanasoff.

Claviceps Tulasne (p. 147)

Sclerotium formed within the hypertrophied tissues of the ovary of the host, succeeding the conidial stage which is a *Sphacelia*; stroma erect, with a long sterile base and a fertile, usually knot-like head; perithecia closely scattered, sunken in the stroma with only the ostiole protruding, flask-shaped, the walls scarcely distinguishable from the stroma; asci cylindric, 8-spored; spores hyaline, continuous. Several species are recorded all affecting the ovaries of the Gramineæ.

***C. purpurea* (Fr.) Tul.**

Sclerotium elongate, more or less curved, and resembling a much enlarged grain, after a period of rest producing few or many, clustered or scattered stromata which are 0.5-1.5 cm. high; spore $60-70 \mu$ long. Conidia (= *Sphacelia segetum*) produced on the grain before the sclerotium is formed, conidiophores short, cylindric, arranged in a compact palisade, bearing small, oval, hya-

line, 1-celled conidia. Hosts, rye, wheat, oats and numerous other grasses.

Infection of the ovary at blooming time is followed by complete possession and consumption of the ovarial tissue by the mycelium,



FIG. 145.—*C. purpurea*. *D*, Sphacelia stage; *E*, germinated sclerotia; *G*, section of stroma; *H*, section of a perithecium, *J*, ascus with spores. After Tulasne.

and by considerable development of stroma beyond the ovary. On the external much-folded part of this stroma, particularly at its distal end, are borne layers of conidiophores, numerous conidia and a sweet fluid is exuded. The conidia, carried by insects, spread summer infection. Later the stroma, losing a large

part of the distal region, rounds off to a definite sclerotium, smooth, firm, blue to black in color, and several times larger than the normal grain of the host plant.

After a period of rest, usually lasting till the following season, the sclerotium gives rise to several stalked, capitate, perithecial stromata. The perithecia are arranged around peripherally, the ostioles protruding and giving the head a rough appearance. The sclerotium constitutes the ergot of pharmacy and contains a powerful alkaloid capable of causing animal disease.

This species is differentiated into a number of biologic races.

C. microcephala (Wallr.) Tul. infects numerous grasses being especially destructive to blue grass.

Two species **C. paspali** S. & H. and **C. rolfii** S. & H. occur on *Paspalum*.

Ustilaginoidea Brefeld (p. 147)

Sclerotium formed in the grain of the host, resembling superficially a smut sorus, in the center composed of closely interwoven hyphæ, externally the hyphæ are parallel, radiating towards the periphery and bearing echinulate, globose, greenish conidia; stroma with a long sterile stem and a fertile head; perithecia immersed in the stroma as in *Claviceps*; asci and spores also as in *Claviceps*.

Two species are known, one on *Setaria* which produces an ascigerous stage, the other on rice, the ascigerous stage of which is not known but which is placed in this genus on account of the similarity of its conidial stage with that of the other species.

U. virens (Cke.) Tak.

Ascigerous stage unknown, sclerotia spherical, about 5 mm. in diameter; conidia spherical, at first smooth-walled, hyaline, at maturity echinulate and olive green, 4-6 μ .

The short thick walled hyphæ of the interior of the sclerotium are closely interwoven to a false tissue, toward the periphery they become parallel and are directed radially. Here a yellow layer is produced and spores are formed laterally on the hyphæ. When mature the spores are in mass dark olive-green and form an outer green layer on the

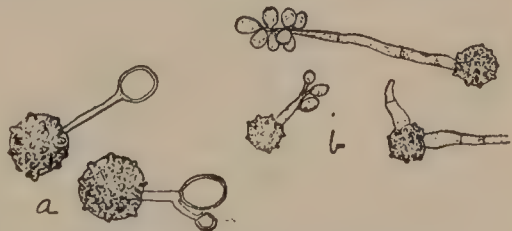


FIG. 146.—*U. virens*; a, spores germinated in water; b, germinated in bouillon. After Fulton.

sclerotium. The spores germinate in water, producing a vegetative mycelium which bears secondary spores and somewhat resembles the mycelium of the Ustilaginales.

Dothideales (p. 95) ¹

Ascomycetes, simple or stromate; ascigerous loculi without a proper membrane.

Conidia of various forms are present.

Though numerous genera occur, only the two following need be mentioned.

Phyllachora Nitschke ^{2, 3}

Stromata in the mesophyll and remaining covered, with cuticular or epidermal clypeus; structure prosenchymatic-dothideoid, or of more or less irregular hyphæ; loculi sunken in the leaf, the apex growing into the clypeus; spores 1-celled, hyaline; paraphysate. Three hundred twenty-two species are given by Theissen & Sydow on many hosts.

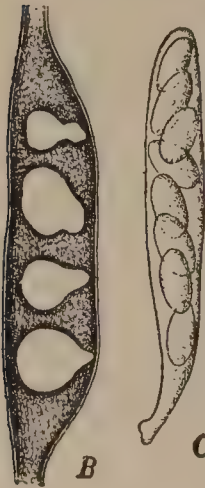


FIG. 147.—*P. graminis*. *B*, stroma in section; *C*, an ascus and spores. After Winter.

P. graminis (Pers.) Fcl. Stromata variable in size and form but usually about 4 x 1 mm., causing conspicuous, black spots on leaves, visible from both sides; locules 186–220 μ in diameter, 145–175 deep; asci short-pedicellate, cylindric, 60–70 x 8–10 μ , 8-spored; spores elliptical, hyaline, 9–11 x 4–5 μ ; paraphyses filiform.

This fungus occurs on many grasses with but slight injury to them. As generally understood it is a collective species which will doubtless be segregated later.

Many other species are recorded on various grasses and one on corn.

¹ Theissen, F. and Sydow, H. Die Dothideales Ann. Myc. **13**: 149, 1915.

² Dalbey, Nora. Phyllachora as the cause of a disease of corn, and a general consideration of the genus Phyllachora. Trans. Ill. Acad. Sc. **10**: 230, 1917.

³ Clevenger, J. F., Notes on some North American Phyllachoras. Jour. Myc. **11**: 159, 1905.

Dibotryon Theissen & Sydow

Loculi closely placed on a compact stroma, free; connected with the stroma by a short basal column which also affords the thin covering of the locules; no ostiole; locules $230\ \mu$ high x $180\text{--}220\ \mu$ broad.



FIG. 148.—*D. morbosum*. *b*, magnified section of a knot showing the perithecia; *c*, conidiophores and conidia; *d*, section of a perithecium showing numerous asci, one of which is shown more highly magnified at *e*; *f*, several of the two-celled ascospores germinating in water. After Longyear.

D. morbosum (Sch.) Theiss. & Sydow^{1, 2}*Plowrightia morbosa* (Schw.) Sacc.

Stromata formed within the tissues of the host plant, erumpent, tubercular or cushion-shaped, depressed or elevated, smooth, later frequently wrinkled, white within; elongate, up to 2 or 3 dm. long; perithecia scattered, often entirely suppressed; asci cylindrical, 8-spored, about 120 μ long; spores 2-celled, hyaline to light green, variously arranged in the ascus, 16–20 x 8–10 μ , ovate, the cells usually unequal; paraphyses filiform.

Conidia (=Cladosporium sp.) produced upon greenish areas on the young stromata; conidiophores erect, flexuose, septate, simple, 40–60 x 4–5 μ ; conidia borne singly at the apex of the conidiophore, obovate, unicellular, light brown, about 6–8 x 2–5 μ .

Hosts: Cultivated sour cherry and plum, wild red and yellow plum, Chickasaw plum, choke cherry, wild red cherry and wild black cherry. Found only in America.

It has been shown that biologic specialization occurs.

The mycelium invades the cambium of twigs, usually in early spring, and from it grows outward into the bark region causing the bark elements to overgrow and the twig to swell slightly during the first summer. With the renewed growth of the following spring the swelling proceeds rapidly. During May to June the mycelium ruptures the bark which is soon lost and a dense fungous pseudoparenchyma is formed. From this the conidiophores appear, forming a velvety growth of olivaceous color. At this period the knot consists largely of a fungous stroma with an admixture of bark elements and even some wood cells.

Later in the season conidiophores cease to form and the knot turns to a black, hard stroma. Perithecia now become easily visible in this black stroma and in January or later the asci mature. That the fungus is the actual cause of the black knot was first demonstrated by Farlow in 1876, though the fungus was described as early as 1821 by Schweinitz.

¹ Formerly known as *Plowrightia morbosa* this species was, together with certain species of *Botryosphaeria* that lack paraphyses, recently moved into a new family, the *Pseudosphaeriales*, by Theissen and Sydow.

² Stewart, A. Some observations on the anatomy and other features of "black knot." *Am. Jour. Bot.* **1**: 113, 1914. See *Annales Mycologi* **16**: 1, 1918.

Sphæriales (p. 95)

Mycelium chiefly confined to the substratum; perithecia variable, usually globose, with a more or less elongated ostiole, hairy or smooth, free on the substratum, more or less deeply sunken, or borne on or sunken in a stroma; asci borne basally, variable in size, opening by a pore; spores variable, globose, ovate to elongate or filiform, hyaline or colored; paraphyses usually present; conidial forms various.

The stromata may vary from a delicate hyphal web to a firm crustaceous structure. The pycnidia are mostly carbonous, black and brittle. Conidia of many forms are present and often constitute the only truly parasitic form of the fungus; the ascigerous form developing only after the death of the part of the host involved.

The order is very large, embracing according to Lindau some eighteen families and over six thousand species.

KEY TO FAMILIES OF Sphæriales

- Perithecia free, either without a stroma, partly seated in a loose mass of mycelium, or sessile above an imperfect stroma
- Walls of the perithecia thin and membranous; asci soon disappearing. Perithecia usually sunken, with only short hairs about the mouth..... 1. **Sordariaceæ**, p. 158.
- Walls of the perithecia coriaceous or carbonous
- Perithecia either entirely free, or with the base slightly sunken in the substratum or stromatic layer
- Stroma wanting or only thread-like or tomentose
- Mouths of the perithecia mostly in the form of short papillæ..... 2. **Sphæriaceæ**, p. 159.
- Mouths of the perithecia more or less elongate, often hair-like..... 3. **Ceratostomataceæ**, p. 164.
- Perithecia without a stroma, and sunken in the substratum, or within a stroma
- Stromata none; perithecia rarely united above by a black tissue (clypeus)
- Asci not thickened at the apex, mostly projecting at maturity. Walls of the

- perithecium thin, coriaceous; mouth mostly short or plane
 Asci clinging together in fascicles, without paraphyses..... 4. **Mycosphærellaceæ**, p. 165.
- Asci not fasciculate; with paraphyses.. 5. **Pleosporaceæ**, p. 178.
- Asci usually thickened apically, opening by a pore; perithecia usually beaked, without a clypeus..... 6. **Gnomoniaceæ**, p. 189.
- Perithecia firmly imbedded in a stroma, the mouths only projecting, or becoming free by the breaking away of the outer stromatic layers
- Stromata fused with the substratum
 Conidia produced in pycnidia..... 7. **Valsaceæ**, p. 199.
- Conidia developed from a flattened surface..... 8. **Melanconidaceæ**, p. 202.
- Stromata formed almost wholly of hardened fungal hyphæ
 Spores rather large, 1 to many-celled, hyaline or brown, conidia mostly in cavities in the stroma..... 9. **Melogrammataceæ**, p. 203.
- Spores 1-celled, rarely 2-celled, blackish brown. Conidia developed on the upper surface of the young stroma..... 10. **Xylariaceæ**, p. 207.

Sordariaceæ (p. 157)

Perithecia superficial or deeply sunken in the substratum, often erumpent at maturity, thin and membranous to coriaceous, slightly transparent to black and opaque; stroma usually absent, if present the perithecia immersed in it with projecting papilli-form beaks; asci usually very delicate, cylindric, 8-spored; spore, usually dark-colored; paraphyses abundant.

A small order, chiefly dung inhabiting.

Acanthorhynchus Shear

Perithecia scattered, submembranous, buried, beaked, the beak with non-septate spines; asci opening by an apical pore; paraphyses present, septate; spores continuous, brownish-yellow.

There is a single species, **A. vaccinii** Sh. which produces rot of cranberries, also leaf spots, but the fructification of the fungus

is rarely found in nature except on old fallen leaves. Remarkable appressoria are produced by the germ tubes from the spores, Fig. 150.



FIG. 149.—A single perithecium of *A. vaccinii* taken from a pure culture on corn meal. After Shear.



FIG. 150.—*Acanthorhynchus*; 16, a germinating ascospore bearing the peculiar appressorium. 17, view from above. After Shear.

Sphæriaceæ (p. 157)

Perithecia single or clustered, free, or with a false stroma in which they are more or less sunken; walls leathery, horny or woody; ostiole rarely elongate, usually papillate; spores frequently appendaged.

The family is distinguished by its free perithecia with papillate ostioles. It contains about seven hundred species.

KEY TO GENERA OF Sphæriaceæ

- Perithecia hairy above, rarely smooth above and hairy beneath
 - Spores 1 or 2-celled; perithecia thick, leathery or carbonous
 - Spores hyaline 1. *Trichosphæria*, p. 160.
 - Spores dark colored, 2-celled 2. *Neopeckia*, p. 161.
 - Spores more than 2-celled
 - Perithecia thin, leathery or cuticularized 3. *Acanthostigma*, p. 161.
 - Perithecia thick, carbonous or woody; spores spindle-form, many-celled, concolorous, hyaline or brown 4. *Herpotrichia*, p. 162.
- Perithecia smooth, neither hairy nor tuberculate; spores 1-celled, dark, unappendaged; perithecia carbonous 5. *Rosellinia*, p. 163.

Trichosphæria Fuckel (p. 159)

Perithecia usually free, globose, woody or carbonous, hairy, ostiole flat or papillate; asci cylindric, 8-spored; spores 1 to 2-celled, hyaline; paraphyses present.

The species are mainly saprophytes.

T. sacchari Mass.

Perithecia broadly ovate, dark-brown, beset with brown hairs; spores elongate-ellipsoid, 1-celled; the conidial forms are various

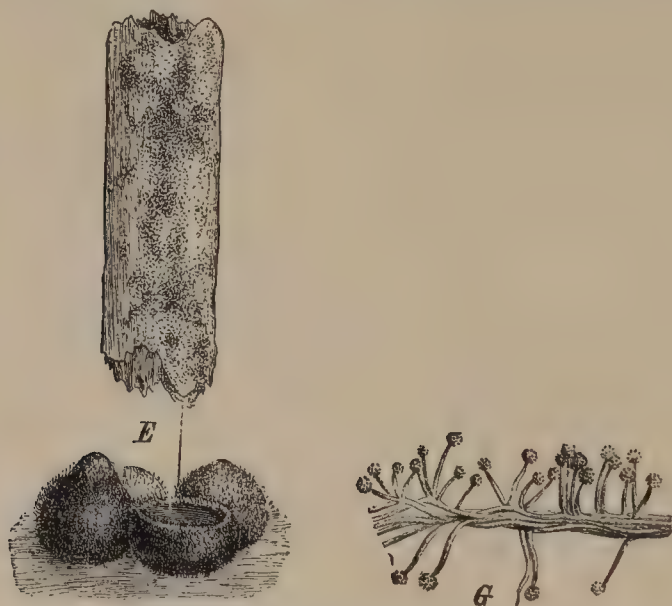


FIG. 151.—*Trichosphæria*. *E*, habit sketch; *G*, conidial stage. After Lindau, Winter and Brefeld.

and their genetic connection is by no means certain. (1) (= *Coniothyrium megalospora*) Pycnidia 1–3, on a dark-colored, parenchymatous stroma; conidia elongate, straight or curved, brownish, $12 \times 5 \mu$, (2) The macroconidia (= *Thielaviopsis ethacetica*) see p. 396, are often found forming intensely black, velvety layers lining cracks and cavities in diseased canes. (3) Microconidia produced on the surface in *Oidium*-like chains. Their connection with this fungus is disputed and uncertain.

It is a sugar-cane parasite.

Neopeckia Saccardo ¹ (p. 159)

Perithecia carbonous, superficial, setose, papillate, asci 8-spored, many-paraphysate; spores dark, 2-celled.

N. coulteri (Pk.) Sacc. *Perithecia* spherical, 0.32–0.5 mm. in diameter, immersed in a dark brown, felt-like subiculum, 0.4–0.53 mm. thick; asci cylindrical, 150–185 x 15–18 μ ; paraphyses filiform, fugacious; spores obliquely uniseriate in the asci, blunt-elliptical, at first pale brownish, later dark-brown, 1-septate, constricted at the septum, 20–29 x 9.5–10 μ .

On living leaves and twigs of pine.



FIG. 152.—*N. coulteri*, a perithecium, ascus and spores. After Sturgis.

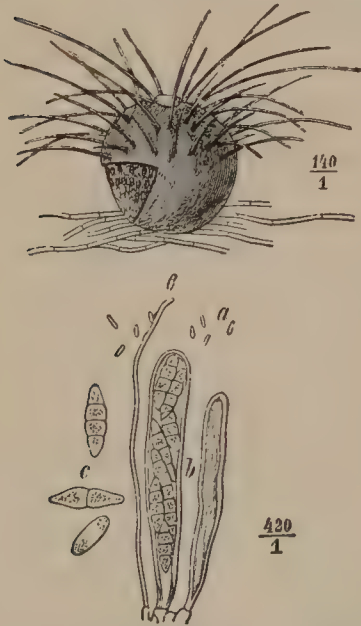
Acanthostigma de Notaris (p. 159)

FIG. 153.—Perithecium of *A. parasiticum*, showing ostiole, bristles, asci, paraphyses and spores. After Hartig.

Perithecia free, globose or ovate, very small; walls leathery, black, beset with stiff bristles, ostiole short; asci usually cylindric, rarely ovate, 8-spored; spores spindle-shaped, multicellular by cross walls, hyaline; paraphyses few or none.

A. parasiticum (Hartig) Sacc.

Perithecia globose, minute, with rigid divergent hairs, 0.1–0.25 mm. in diameter; asci 50 μ long, early disappearing; spores fusoid, straight or curved, smoky, 15–20 μ , continuous or 2 to 3-septate.

Common on leaves of fir, hemlock and other conifers. The hyaline mycelium grows on the lower sides of branches and on the leaves killing them and matting them to the branches. The mycelial cushions later

turn brownish and eventually very small perithecia form on them.

¹ Sturgis W. C. *Herpotrichia and Neopeckia on Conifers*. *Phytop.* **3**: 152, 1913.

Herpotrichia Fuckel (p. 159)

Perithecia superficial, globose or subglobose, texture firm, coriaceous to subcarbonous, hairy or smooth, ostiole papillate or not; asci oblong to clavate; spores fusiform, 2 or many-celled, hyaline or brown; paraphyses none.

The species, numbering about twenty-five and growing on woody plants, are mostly saprophytes.

H. nigra (Pk.) Sacc.

Perithecia spherical with slightly prominent ostiole, 0.25–0.45 mm. in diameter, semi-immersed in a dark brown, felt-like subiculum, 0.27–0.5 mm. thick; asci

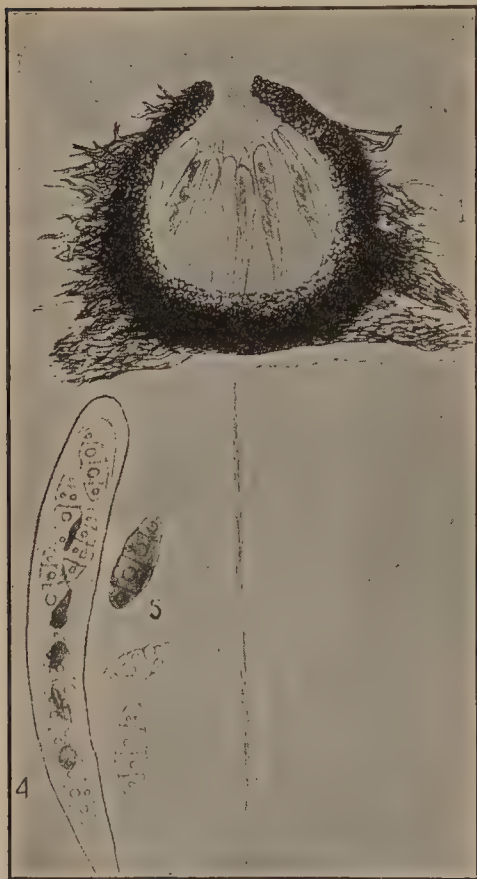


FIG. 154.—*H. nigra*, a perithecium, ascus and spores.
After Sturgis.



FIG. 155.—*Herpotrichia*.
B, ascus; *C*, spore.
After Winter.

club-shaped, 128–155 x 14–18 μ ; paraphyses filiform, fugacious; ascospores irregularly biserial in the asci, elliptical, at first 1 to 3-septate, hyaline, later 3-septate, more or less constricted at the septa, pale to darker olivaceous-brown, 22–33 x 8.5–9 μ ; conidia borne singly on short hyphae, dark brown, 3 to 6-septate, constricted at the septa, 27.5–29 x 9–10 μ .

On living leaves and twigs of spruce, pine, juniper and fir.

A felt-like growth of dark brown mycelium spreads over the affected leaves killing them and portions of the branches.

Rosellinia Cesati & de Notaris (p. 159)

Perithecia superficial, but often with the bases more or less sunken in the substratum, coriaceous or carbonous; brittle, spherical or ovate, bristly or not; asci cylindric, 8-spored; spores elliptic, oblong or fusiform, 1-celled, brown or black; paraphyses fusiform. Conidia of the type of *Coremium*, *Sporotrichum*, etc.

In most cases the active parasitic stage occurs on roots and consists of a vigorous white mycelium, which remains for a long time sterile, developing large branching and interlacing rhizomorphs (*Dematophora*) which later become brown. These resemble somewhat, but are distinguishable from, the rhizomorphs of *Armillaria mellea*; again, they are *Rhizoctonia*-like.

There are over one hundred seventy species; mostly saprophytic.

R. necatrix (Hart.) Berl.

A destructive fungus, long known as *Dematophora necatrix*, possesses a white mycelium which invades the small roots, thence passes to larger ones, extending in trees through the cambium and wood to the trunk, occasionally rupturing the bark and producing white floccose tufts. Sclerotia of one or more kinds are produced in the bark and often give rise to conidia on tufted conidiophores in a *Coremium*-like layer (Fig. 156). The mycelium, when old, turns brown and produces large branching, interlacing rhizomorphic strands which spread to the soil, or wind about the roots.

Perithecia found on old wood, long dead from such attack, belong to the genus *Rosellinia* and are believed to present the as-



FIG. 156.—*R. necatrix*. 4, coremium and conidia; 5, perithecia extruding spores; 6, asci and paraphyses. After Hartig, Prillieux and Viala.

cigerous form of *Dematophora necatrix*. Similar claims of relationship of this fungus to several other genera have been made and its actual position cannot be considered as established with certainty.

The fungus attacks many kinds of plants.

R. caryæ Bonar.¹ Perithecia superficial or slightly sunken in the outer bark, scattered or gregarious, carbonaceous, brittle, slightly bristly or smooth, broadly flask-shaped, with a short distinct ostiole; asci cylindric; 8-spored, averaging $50 \times 6-8 \mu$; spores uniseriate, sub-globose, one celled, dark brown, $5-7 \times 3.5-4.5 \mu$; paraphyses filiform.

Conidia = *Dothichiza caryæ* Bonar. Pycnidia scattered, erumpent, dome-shaped, non-ostiolate, irregularly dehiscent, wall distinct except at base, hymenial layer continuous over the inner surface, conidiophores short; spores 1-celled, hyaline, broadly fusoid, $5-7 \times 2.5-3 \mu$. The cause of canker on *Carya*.

R. massinkii Sacc. was reported by Halsted on hyacinth bulbs.

R. quercina Hartig is parasitic on roots and stems of young oaks.

R. radiciperda Mass., closely allied to *R. necatrix*, affects a large number of hosts, among them apple, pear, peach, cabbage, and potato.

Ceratostomataceæ (p. 157)

The fungi of this family are very similar to the *Sphæriaceæ*, but are distinguished by less pronouncedly carbonous perithecia which may be merely membranous, and open by an elongate, beak-like ostiole. It is a family of only about one hundred twenty-five species, chiefly saprophytes.

Ceratostomella Saccardo

Perithecia superficial, firm; asci ovate, 8-spored, disappearing early; spores elongate, blunt or pointed, 1-celled, hyaline. About thirty species. An extensive study of the genus was made by Hedgcock who recognizes several species as discoloring lumber.

C. pilifera (Fr.) Wint. has been described in detail by von Schrenk as the cause of a blue color in pine wood.

¹ Bonar, Lee. The life history of *Rosellinia Caryæ* Sp. Nov. causing a hickory canker and disease. *Phytop.* **12**: 381, 1922.

Mycosphærellaceæ (p. 158)

Perithecia mostly subepidermal, rarely subcuticular, finally more or less erumpent or even superficial, membranous or leathery, fragile; asci fasciculate, 8-spored; spores variable, septate, rarely muriform, hyaline to dark-brown; paraphyses none.

This family of over seven hundred species contains many saprophytes and several very important parasites.

KEY TO GENERA OF *Mycosphærellaceæ*

Spores 1-celled or not clearly 2-celled

Perithecia very small, on a basal growth of thick branched hyphæ.....

1. *Ascospora*, p. 165.

Perithecia without such a basal growth, spores usually unequally 2-celled...

2. *Guignardia*, p. 166.

Spores 2-celled

Perithecia produced on living plants....

3. *Stigmatea*, p. 171.

Perithecia appearing only after the death of the host.....

4. *Mycosphærella*, p. 171.

Spores several-celled, hyaline

Spores elongate transversely divided, many celled.....

5. *Sphærulina*, p. 177.

Spores muriform.....

6. *Pleosphærulina* p. 177.

***Ascospora* Fries**

Perithecia borne on a subiculum of thick, brown, much-branched hyphæ, globoid, black, carbonous; asci clavate, clustered, 8-spored, small; spores 1-celled, hyaline; paraphyses none.

A. beyerinckii Vuil. Perithecia black, depressed-globose, apapillate; ostiole indistinct or absent, 100–130 μ in diameter; spores elliptic-fusoid, ends obtuse, continuous, hyaline, guttulate, 15 x 5–7 μ .

Conidia, 1. (= *Phyllosticta beyerinckii*) pycnidia globoid with hyaline spores.

Conidia, 2. (= *Coryneum beyerinckii*) conidio-

phores short, crowded, from a minute subepidermal stroma; conidia single, elliptic-oblong, 1 to 5-septate, brown, about 36 x 15 μ . On drupaceous hosts, especially the peach, causing spots on the leaves, fruit and shoots, accompanied by a gummy exudate.

In spots on the bark the mycelium is often sterile, but when it becomes old distinct pustules usually show in a well developed subepidermal stromatic tissue and from these pustules, as they



FIG. 157.—*Ascospora himantia*. Asci. After Winter.

rupture the epidermis, the conidiophores are produced. Conidia usually abound on the surface of twigs which have borne affected leaves. They germinate readily and produce either a sooty super-

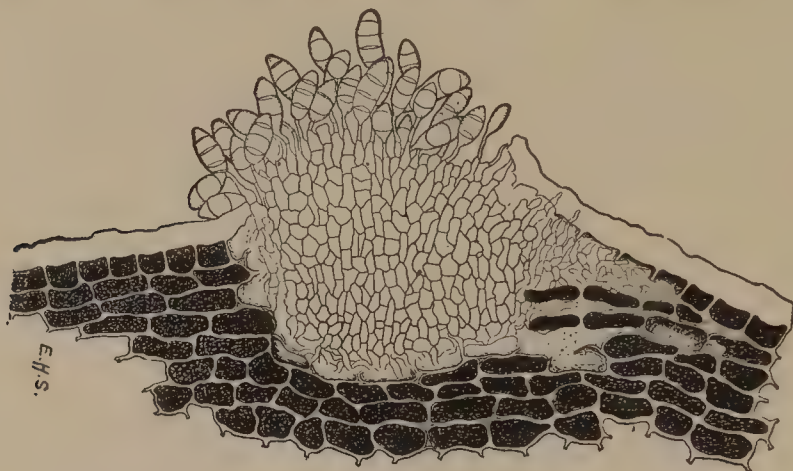


FIG. 158—Section through a *Coryneum* pustule on peach. After Smith.

ficial mold or if on new bark enter the host tissue and induce spotting.

The conidial stage (*Coryneum*) of the fungus was grown in artificial culture by Smith but no ascigerous stage was found.

***Guignardia* Viala & Ravaz (p. 165)**

Perithecia sunken, globoid or flattened, black, leathery; ostiole flattened or papillate; asci clavate, 8-spored; spores ellipsoid or fusiform, hyaline, somewhat arched, 1 or 2-celled; paraphyses none.

Over one hundred thirty species are known. Some are important parasites.

Conidial forms are found in *Phyllosticta* and *Phoma*.

***G. bidwellii* (Ellis) V. & R.**

Perithecia minute, globose, subepidermal, erumpent, perforate; asci clavate-cylindric, obtuse, 60–70 x 10–13 μ ; spores elliptic to oblong, continuous, 12–17 x 4 $\frac{1}{4}$ –5 μ .

Conidia (= *Phoma uvicola*, *Phyllosticta labruscæ*) borne in pycnidia 180 x 180 μ , subepidermal, elliptic, thick-walled; conidiophores short, simple; conidia ovate to elliptic, 8–10 x 7–8 μ . Filiform microconidia "spermatia" are borne in flask-shaped pycnidia, 0.1–0.2 x 0.45–0.46 μ .

The fungus has been placed successively in the genera *Sphæria*, *Physalospora*, *Læstadia* and *Guignardia*.

Perithecia were first found in 1880 by Dr. Bidwell in New Jersey. They are abundant on berries which have wintered out of doors.

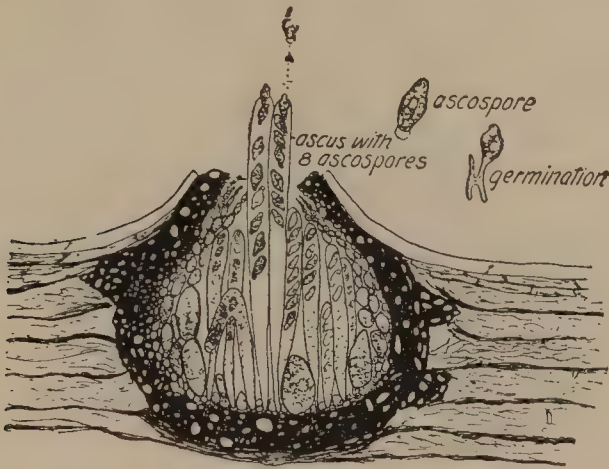


FIG. 159.—Diagrammatic section of a perithecium containing ascospores. Germination of a spore at the right. After Reddick.

It is found on all green parts of *Vitis* and *Ampelopsis*, the as-cigerous stage common only on the mummified fruits. The mycelium kills the host cells and causes collapse of the spongy parenchyma.

Reddick describes the development of the spots essentially as follows:

On the leaves the first evidence of the spot is the slight blanching of a single one of the smaller areolæ of the leaf. Soon the blanching extends to adjacent areolæ, and if an areola is entered it is usually entirely involved. The small veinlets form the margin of the spot so that the outline is finely crenulate. By the time the spot is .3 to .4 mm. in diameter it has a cinereous appearance. The margin, while sharply defined, is not changed in color. By the time the spot is 1 mm. in diameter, the margin appears as a black line, while the remainder of the spot is grayish-brown. A little later the margin is a brownish band and the brown gradually extends inward until the whole spot is covered. As soon as the brown band attains some width the blackish line on the margin is to be seen again. A second wave of deeper brown may pass across the spot but sometimes leaves a marginal band of a deeper brown than

the central disc. Spots vary in size from 1 mm. up to 8 mm. in diameter, but in general are 3 to 5 mm. or larger. Occasionally the whole leaf is destroyed but this the result of the coalescence of

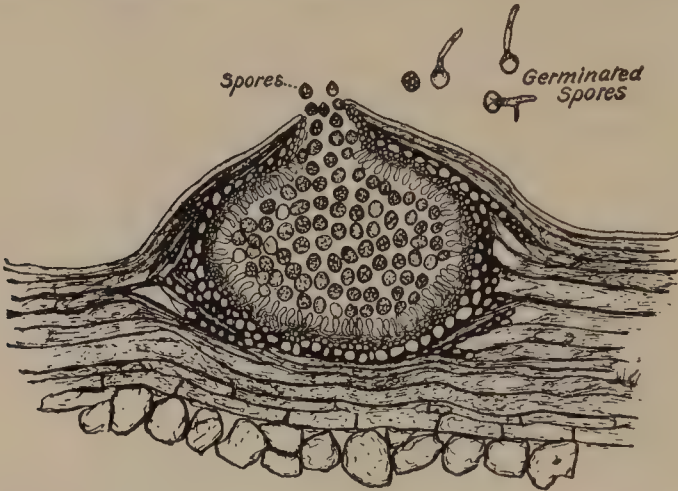


FIG. 160.—Diagrammatic section through a pycnidium, showing how the spores are produced and how they germinate. After Reddick.

many spots. When the spot has attained full size pycnidia protrude from under the cuticle and either dot the entire surface of the spot with minute specks or are more often confined to a more or less concentric ring. The different shades of color are apparent on

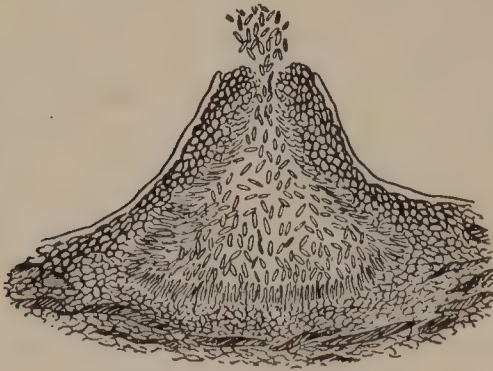


FIG. 161.—Section of a pustule showing microconidia. After Longyear.

the under side of the leaf on such varieties as have leaves which are smooth beneath. The pycnidia, however, have never been seen on the under side of the leaf in our varieties.

On stems, tendrils, peduncles, petioles and leaf veins the spot in its first appearance is a small darkened depression which soon becomes very black. On a cane the lesion rarely extends more than a quarter of the way round, while on a tendril or leaf petiole it may extend from half to all of the way round. On shoots, the lesions never extend so deep as to cut off the sap supply, but on petioles

this occasionally happens, rarely so on peduncles, and quite commonly so on pedicels and tendrils. The first indication of Black Rot on the berry is the appearance at some point of a small circular blached spot, scarcely 1 mm. in diameter. The blanching is so slight as to be detected only by careful observation. It rapidly becomes more apparent, due to the appearance of a brownish line at the margin. The whitish center increases in size and the brownish or reddish-brown ring increases in diameter as well as in width and is quite evident when the spot is 2 mm. in diameter. When the spot is 3 mm. in diameter the ring is one-half mm. in width and enough darker to give a bird's eye effect (a light circular disc with an encircling darker band). The spot rapidly increases in size so that in twelve hours more it may be 6 to 8 mm. in diameter, and the encircling band nearly 2 mm. in width. After five hours more, the spot is 8 or 9 mm. in diameter and there begins to appear an outer darker band and an inner light brown one which have in some cases a much lighter line between them. The aureola is thus composed of two or three bands or rings. Eighteen hours later the spot is 1 cm. or more in diameter, is distinctly flattened, and numerous minute brown specks appear on the white center of the spot. In five hours more they are so numerous as to give a blackish appearance. In New York, Reddick found that the asci began to ripen in May and continue to mature throughout the summer, being still abundant in October.

The asci swell in water, often to twice the length given above; spores are forcibly ejected from the asci at maturity, being thrown to a height of 2 to 4 cm. There is at one end of the ascospore a hyaline vesicle which probably aids in fixing it to the host. They germinate but slowly, requiring from thirty-six to forty-eight hours to show germ tubes. Reddick determined the incubation period on fruit as from eight to twenty-one days and found that only tender leaves, still growing, are susceptible. The berry is susceptible even after the calyx has fallen. The pycnidial spores are said by some to show a hyaline appendage though others by careful study fail to find it. These spores often live

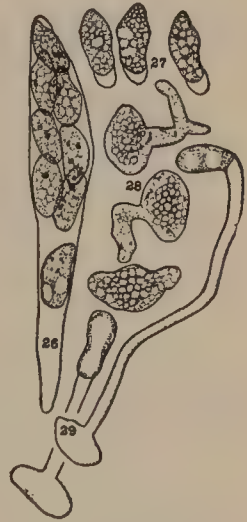


FIG. 162.—*G. bidwellii*; 26, nearly mature ascus with spores; 27, mature ascospores; 28, germinating ascospores, 29, same with appressoria. After Reddick.

over winter. The microconidia which develop in pycnidia similar to those of the macroconidia do not occur so abundantly early in the season as they do later and seem to be mainly limited to the fruits. Sporeless pycnidia, **pycnosclerotia**, also occur and may eventually develop into perithecia. Conidia on hyphæ, of questionable relationship to the fungus, are sometimes seen.

Reddick secured pure cultures in the following ways.

1. In poured plate dilution of asci; some twenty days were required.

2. By inverting a plate of sterile agar over a bunch of mature mummies floating on water. The ejected ascospores thus clung to the agar and gave pure cultures in ten days.

3. By aseptic transfer of the mycelium.

4. By aseptic transfer of pycnospores.

Artificial infections have been reported in Europe from both conidia and ascospores; Reddick, who made many thousand inoculations under all conceivable conditions, failed utterly of positive results.

G. vaccinii Sh.

Perithecia on young fruit or flowers, subepidermal, globose, walls thick, carbonous; asci clavate, 60–80 μ long; spores elliptic or subrhomboidal, hyaline, becoming tinted.



FIG. 163.—A vertical section of a perithecium of *Guignardia vaccinii*, showing asci. After Shear.

Conidia (= *Phyllosticta*) borne in pycnidia similar to the perithecia but thinner-walled, 100–120 μ ; conidia hyaline, obovoid, 10.5–13.5 x 5–6 μ . On *Vaccinium*.

In the decaying berries all sporing forms of the fungus are rare though in the softened tissues fungous hyphæ abound. Transferred to culture media these hyphæ grow readily and produce spores abundantly.

G. æsculi (Pk.) Stew.¹

Perithecia 175 μ broad, covered by epidermis; asci subclavate; spores hyaline, 7–10 x 5–6 μ . Conidia (= *Phyllosticta paviæ* Desm. = *P. sphæropsidea* E. & E.) epiphyllous; spots reddish-brown, scattered or confluent, 1–2 cm.; pycnidia scattered, immersed, punctiform, erumpent above, subepidermal; conidia globose to broadly ellipsoid, hyaline, 12–15 x 8–10 μ .

On horse chestnut causing leaf spot.

¹ Stewart, V. B. The leaf blotch disease of horse chestnut. *Phytop.* 6: 5, 1916.

Stigmatea Fries (p. 165)

Perithecia subepidermal, or subcuticular, thin, black; asci oblong, subsessile, 8-spored; spores ovoid-ellipsoid, 2-celled, yellowish or hyaline; paraphyses present. The ascigerous stage of two species of *Entomosporium* are said by Lindau to belong to this genus. Atkinson, however, places them in the genus *Fabræa*, see p. 112.

S. juniperi (Desm.) Wint., is found on living leaves of *Juniperus* and *Sequoia*.

Perithecia scattered, lenticular or subhemispheric, rough, 200–300 μ in diameter, asci rounded and obtuse above, abruptly tapering below into a short stipe, 60–70 x 20 μ ; spores ovate-lanceolate, unequally 2-celled, yellowish-hyaline, 16–25 x 6–8 μ .

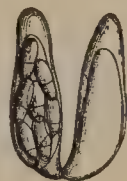


FIG. 164.—*Stigmatea*.
Asci and spores.
After Winter.

Mycosphærella Johans.¹ (p. 165)

Sphærella Ces. & De Not.

Perithecia subepidermal, suberumpent, globose-lenticular, thin, membranous, ostiole depressed or short papillate; asci cylindric to clavate, 8-spored; spores hyaline or greenish, ellipsoid, 2-celled; paraphyses none.

This large genus of over five hundred species contains several serious plant pathogens. It is often found in its conidial forms as: *Ramularia*, *Ascochyta*, *Septoria*, *Phleospora*, *Cercospora*, *Ovularia*, *Cylindrosporium*, *Phyllosticta*, *Graphiothecium*, *Phoma*, *Diplodia*, or *Septoglœum*. In many cases the relationship of the ascigerous and conidial forms is as yet but imperfectly known. The perithecia are usually found late in the season, often only on leaves that have borne the conidial stage in the summer and have then wintered.

M. fragariæ (Schw.) Lind.

Perithecia on leaves are produced late in the season, globose, subepidermal, membranous, black, thin-walled; asci few, clavate, 8-spored, 40 μ long; spores hyaline, 2-celled, with acute tips, 15 x 3–4 μ .

Conidia (= *Ramularia tulasnei*) abundant in early summer on reddish spots, stromatic, conidiophores simple; conidia elliptic, 20–40 x 3–5 μ , 2 to 3-celled. On strawberry.

The life history was first studied in 1863 by the Tulasne brothers

¹ Grove, W. B. *Sphærella* vs. *Mycosphærella*. Jour. Bot. **40**: 89, 1912.

under the name *Stigmatea*. The generic name was changed to *Sphaerella* in 1882 and later to *Mycosphaerella*, because the name *Sphaerella* was preoccupied by an algal genus.

The slender mycelium pervades the diseased areas disorganizing the host cells and resulting in reddish coloring of the sap. Observations indicate that the mycelium or portions of it can remain alive over winter in the host tissue ready to produce abundant conidia in the spring.

The common conidial stage is the *Ramularia*-form which abounds all summer. Sowings of these conidia, under conditions of humid atmosphere, result in characteristic spots in from ten to eighteen days. Toward winter sclerotial bodies are formed from the mycelium. These in culture dishes have been seen to produce the typical summer conidia. Some of these sclerotia-like bodies have been reported as "spermogonia," bearing numerous "spermatia" $1 \times 3 \mu$. Perithecia abound in autumn. These are larger than the spermogonia and are usually embedded in the leaf tissue, though they sometimes appear superficially. Conidiophores are often borne directly on the perithecium wall. Ascospores germinate within the ascus. From the mycelium resulting from ascospores typical summer conidia have been secured.

M. grossulariæ (Fr.) Lind.

Perithecia hypophyllous, gregarious, spherical, with minute ostiole, black; asci short-pedunculate, clavate, $55-66 \times 8-12 \mu$; spores fusoid, filiform, curved or straight, uniseptate, hyaline, $26-35 \times 3-4 \mu$.

On the gooseberry, conidia=*Septoria ribis* Desm.

M. rubina (Pk.) Jacz.

Perithecia minute, gregarious, submembranous, obscurely papillate, subglobose or depressed, erumpent, black; asci cylindric, subsessile, $70-80 \times 10-12 \mu$; spores oblong, obtuse, uniseptate, generally constricted in the middle, $15 \times 6-7 \mu$, upper cell broadest.

Conidia (=Phoma) are associated with the perithecia and are supposed to be genetically connected with them as is also a second spore form (=Coniothyrium).

The species is held responsible for bluish-black spots on raspberry canes.

M. cerasella Aderh. is reported as the perithecial stage of *Cercospora cerasella* common on cherry.

M. aurea Stone, on *Ribes*, has as a conidial stage, *Septoria aurea* E. & E.

M. rubi Roark.¹

Perithecia mainly hypophyllous, usually gregarious, erumpent, globose, 60–80 μ in transverse diameter with a short papilliform ostiole; asci aparaphysate, eight-spored, 42–45 x 8–10 μ ; ascospores hyaline, fusiform, of two equal cells, straight or slightly curved, 20–25 x 3.50–4.25 μ ; conidial stage (= *Septoria rubi* West.) The cause of leaf spots on *Rubus*.

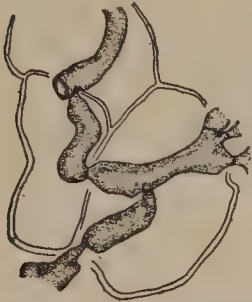


FIG. 165.—*M. nigerristigma*. Mycelium within the cells of the host leaf, showing constrictions where passing through walls of host cells. After Higgins.

M. nigerristigma Higgins. Perithecia black, on spots killed by pycnidial mycelium or scattered over the entire leaf, 90–110 x 45–85 μ , immersed, with the short beak protruding; asci clustered, aparaphysate, 35–45 x 7 μ ; spores fusiform, colorless, 1-septate, 16–21 x 2.5–3 μ .

Pycnidial stage: spots at first glaucous but soon turning brown, often dropping out, 2–5 mm. in diameter; pycnidia colorless or light brown, amphigenous, immersed, globose, with a single large ostiole; spores colorless, long, slender,

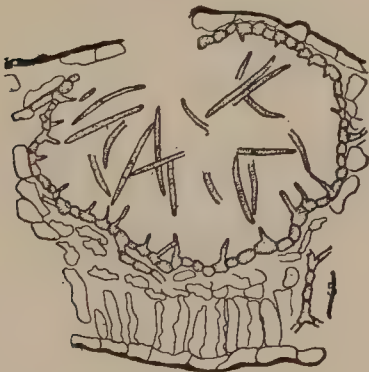


FIG. 166.—*M. nigerristigma*. Mature pycnidium. After Higgins.

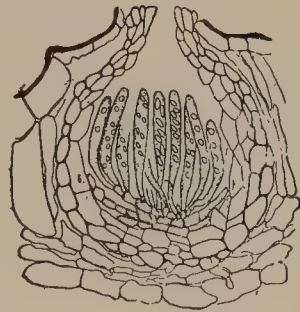


FIG. 167.—*M. nigerristigma*. Mature perithecium with asci and spores in various stages of development. After Higgins.

flexuous, 35–56 x 2–3 μ , continuous or 1 to 4-septate. “Spermatia” produced in “spermogonia” or in the pycnidia in late autumn, 4–5 x 1 μ .

Pycnidial stage parasitic in leaves of *Prunus pennsylvanica*, ascogenous stage saprophytic in leaves of the same host.

M. sentina (Fr.) Schr.

¹ Roark, E. W. The *Septoria* leafspot of *Rubus*. *Phytop.* **11**: 328, 1921.

Perithecia, 80–110 μ ; on dead spots of leaves, the long ostiole erumpent; asci clavate, 60–75 x 11–13 μ , colorless; spores fusiform, curved or straight, 26–33 x 4 μ .

Conidia (=Septoria piricola) borne in pycnidia which are similar in size and form to the perithecia; conidia filiform, curved, 3-celled, 40–60 x 3 μ . On pear and apple.

The conidial form was mentioned in America as early as 1897 by Atkinson. The ascigerous stage was demonstrated, by Klebahn in 1908.

The pycnidia, mainly hypophyllous, are sunk deeply into the leaf tissue and are surrounded by a delicate pseudoparenchyma. The conidia are distinctly tinted, green or smoky.

The perithecia are numerous, and crowded on grayish spots, hypophyllous, on old wintered leaves. They are without stroma. Klebahn by inoculations (June, 1904) with ascospores secured spots in fifteen days and pycnidia in twenty-nine days, bearing the characteristic conidia. From ascospores he also made pure cultures which soon developed pycnidia with conidia.

M. citrullina (C. O. Sm.) Gros.



FIG. 168.—*M. sentina*.
Conidial layer, conidiophores and conidia. After Klebahn.

Perithecia roughish, dark-brown or black, depressed-globose to inverted top-shaped, usually with a papillate ostiole, densely scattered, erumpent, 100–165 μ ; asci cylindric to clavate, 45–58 x 7–10 μ ; spores hyaline, oblong-fusoid, constricted at the septum.

Conidia (=Diplodina citrullina). Pycnidia similar to the perithecia, spores 2-celled, hyaline, straight or curved, more or less cylindric, 10–18 x 3–5 μ .

The fungus was isolated in pure culture by Grossenbacher from muskmelons by direct transfer of diseased tissue to potato agar. Inoculations from these cultures proved the fungus capable of entering healthy uninjured tissue, the disease showing about six days after inoculation. The brownish pycnidia originate from an extensive subepidermal, partially cortical, much-branched, brownish mycelium but soon break through and appear almost superficial. When moistened spores issue in coils. Darker perithecia, nearly superficial, are found on old diseased spots. Both ascospores and conidia are capable of causing infection. Inoculations on pumpkin and watermelon gave positive results.

M. tabifica (P. & D.) Johns.

Perithecia rounded, brown; asci oblong-clavate, 8-spored; spores hyaline, upper cell larger, $21 \times 7.5 \mu$.

Pycnidia (=Phoma) subglobose; conidia elliptic, hyaline, $5-7 \times 3.5 \mu$, escaping as a gelatinous cirrus.

This conidial form, common on beets causing leaf spot throughout the summer, is said to be connected with *M. tabifica* the perithecial form, which is found upon the dead petioles at the end of the season. The conidial stage is variously known as

Phoma betæ, *Phoma sphærosperma*, *Phyllosticta tabifica*. The *Phoma*-form from stems and rotten roots and the *Phyllosticta*-forms from leaves were both studied in pure cultures on many media and many inoculations were made, all leading to the conclusion that the *Phoma* and the *Phyllosticta* are identical.

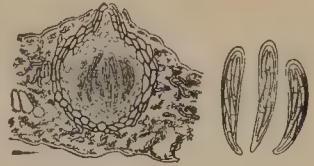


FIG. 169. — *M. sentina*, perithecium and asci. After Klebahn.

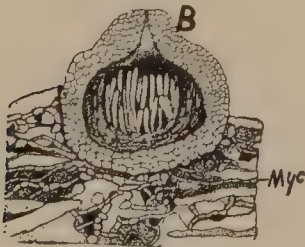


FIG. 170.—*M. citrullina*, A, pycnidium (*Diplodia*) in section, B and C, perithecium and an ascus and spores. After Grossenbacher.

M. tulasnei Jacz.

Perithecia subglobose, minute; asci cylindric fusoid; spores oblong, rather pointed, upper cell in the ascus somewhat larger than the others, $28 \times 6.5 \mu$.

Conidia of two kinds, (1) (= *Cladosporium herbarum*) tufts dense, forming a velvety blackish-olive, effused patch, conidiophores erect, septate, rarely branched, often nodose or keeled;

conidia often in chains of 2 or 3, subcylindric pale-olive, 1 to 3-septate, $10-15 \times 4-7 \mu$. (2) (= *Hormodendrum cladosporioides* Sacc.) Hyphæ erect, simple, bearing apically or laterally a tuft of small, elliptic, continuous, brown conidia in simple or branched chains.

It is the cause of serious disease of cereals and is found also parasitic on pea, apple, raspberry, cycad, agave and as a saprophyte almost anywhere.

M. gossypina (Atk.) Earle

Perithecia ovate, blackish, partly immersed, $60-70 \times 65-91 \mu$; asci subcylindric, $8-10 \times 40-45 \mu$; spores elliptic to fusoid, constricted at the septum, $3-4 \times 15-18 \mu$.

Conidia (= *Cercospora gossypina*); hyphæ flexuose, brown, $120-150 \mu$ high; conidia attenuate above, 5 to 7-septate, hyaline, $70-100 \times 3 \mu$. On cotton.

The intercellular mycelium is irregular, branched, septate, and produces tuberculate stromata from which the brownish hyphæ arise. The perithecia, much less common, are partly immersed in old leaves.

M. pinodes (Berk. & Blox.) Stone.¹ Perithecia numerous, $100-140 \mu$; asci oblong-cylindric, $58-62 \times 12 \mu$; spores 2-rowed, $14-16 \times 5 \mu$.

Pycnidia (= *Ascochyta pisi*).

Spots variable in size, roundish, yellowish with brown margin; pycnidia centrally located, black, of angular cells, $5-7 \mu$; ostiole rounded, surface reddish brown.

On peas, beans, vetch, Cercis, etc. The pycnidia are visible on the dead areas of the stems, leaves, pods or seeds. The mycelium hibernates in affected seeds, reduces their germinating power and carries the fungus over to the succeeding crop.

Inoculations with ascospores have resulted in about five days in characteristic brown lesions resembling in every way those caused by *Ascochyta pisi*. In ten days pycnidia with mature *Ascochyta* spores were obtained.

M. ontarioensis Stone (= *Ascochyta lathyri*) occurs on *Lathyrus* (grass pea).

M. brassicicola (Duby) Lindau (= *Phyllosticta brassicicola* McAlpine) occurs on cabbage and cauliflower causing leaf spot.

M. ulmi Kleb. This is the ascigerous stage of *Phleospora ulmi*

¹Stone, R. E. The life history of *Ascochyta* on some leguminous plants. *Ann. Myc.* 10: 564, 1912.

(Fr.) Wallr. = *Septogloeum ulmi* (Fr.) Bri. and Cav. On elm numerous, small, reddish-brown spots appear on the upper side of the leaves, which gradually turn yellow, the margin becomes brown and rolls up, and the leaves fall early in the season. The spores ooze out in minute cirri which dry on the lower side of the leaf surface and form small whitish patches.

M. rosigena E. & E.

Amphigenous on reddish-brown, purple-bordered spots which are about 3–4 mm. in diameter; perithecia thickly scattered over the spots, minute, 60–75 μ , partly erumpent, black; asci subclavate to oblong, 25–30 x 8–10 μ ; spores biseriate, clavate-oblong, hyaline, 1-septate, 10–12 x 2 μ , ends subacute.

It causes leaf spots of rose.

Other species are on quince, grape, Citrus, sugar-cane, rice, Morus, oak, lime, hazel, beech, balsam, yew, larch, coffee, Poplar, pecan, Hedera, Ficus elastica, primrose, lilies, gladiolus, ferns.

Sphærulina Saccardo (p. 165)

Perithecia globose, membranaceous, ostiolate, asci aparaphysate, 8-spored; spores cylindrical or oblong, 3 to many-septate, hyaline.

S. trifolii E. Rostr.¹

Spot circular, 2–3 mm. in diameter; perithecia epiphyllous; asci 8-spored; spores hyaline, oblong, 3-septate, 32–33 x 12–15 μ . The disease on various clovers is exhibited at first as minute, black lesions on the leaf blades, petioles and stipules, often the leaflets turn yellow and fall. Later these small spots enlarge and have a light brown to gray center surrounded by a dark reddish-brown margin; lesions occur also on the peduncle, calyx and corolla.

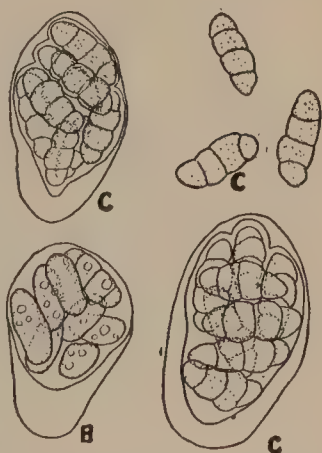


FIG. 171.—*Sphærulina trifolii*: B, an immature ascus from white clover. C, mature asci and ascospores. After Hopkins.

Pleosphærulina Passer (p. 165)

Perithecia subepidermal, erumpent, small, globoid or lenticular, black; asci 8-spored, clavate; spores muriform, hyaline; paraphyses none.

¹ Hopkins, E. F. The *Sphærulina* leafspot of clover. *Phytop.* **13**: 117, 1923.

P. briosiana Pol. Perithecia few, immersed then erumpent; asci paraphysate, 80-90 x 30-40 μ ; spores oblong-fusoid, 3-4 transverse septa, often with 1-2 longitudinal septa, 20-25 x 6-8 μ .

The cause of a spot on alfalfa and clover.

Pleosporaceæ (p. 158)

Perithecia sunken, at length erumpent, or from the first more or less free, membranous or coriaceous, usually papillate; asci clavate-cylindric, double-walled; spores variable, but usually colored, oblong, fusoid or elliptic; paraphyses present.

An order of some nineteen hundred species most of which are saprophytes, although several are parasites, some of considerable importance.

KEY TO GENERA OF Pleosporaceæ

- Spores 1-celled, unappendaged, elongate,
hyaline or light yellow 1. *Physalospora*, p. 178.
- Spores 2-celled.
Perithecia hairy; spores hyaline or brown 2. *Venturia*, p. 182.
Perithecia smooth; not stromatic, spores
brown
Aparaphysate 3. *Didymellina*, p. 184.
Paraphysate 4. *Didymosphæria*, p. 184.
- Spores more than 2-celled, not muriform
Spores elongate, not appendaged
Spores fusoid or elongate, blunt, never
filiform or separating into cells
Spores 3 to many-celled, hyaline or
brown
Spores without thick episporium,
elongate, perithecia smooth;
spores yellow or dark-brown 5. *Leptosphæria*, p. 184.
- Spores filiform, often separating into
cells; perithecia smooth 6. *Ophiobolus*, p. 186.
- Spores muriform, asci 8-spored, spores not
appendaged
Perithecia hairy 7. *Pyrenophora*, p. 189.
Perithecia smooth 8. *Pleospora*, p. 188.

Physalospora Niessl.

Perithecia subglobose, covered, membranous or coriaceous, black, with the ostiole erumpent; asci clavate-cylindric; spores ovoid or oblong, continuous, hyaline or subhyaline; paraphyses present.

This genus contains over one hundred thirty species, a few of which are parasitic on twigs and leaves. Some species possess a *Glœosporium* as the conidial form.

***P. cydoniæ* Arn.** (= *Sphæroopsis cydoniæ* C. & E. = *Sphæroopsis malorum* Pk.)

Perithecia scattered, astromate, buried, with a short protruding, papillate ostiole, globose, 180–235 μ high, 300–400 μ broad; asci usually 8-spored, paraphysate, clavate, 21–32 x 130–180 μ , apex thickened, spores elliptical, 11–15 x 23–24 μ , hyaline to greenish-yellow. Pycnidia usually scattered, 200–300 μ , ostiolate. Conidiophores 8–30 μ long; spores 7–16 x 16–36 μ , brown, ellipsoidal,



FIG. 172.—*Physalospora*. Perithecia and ascus. After Winter.

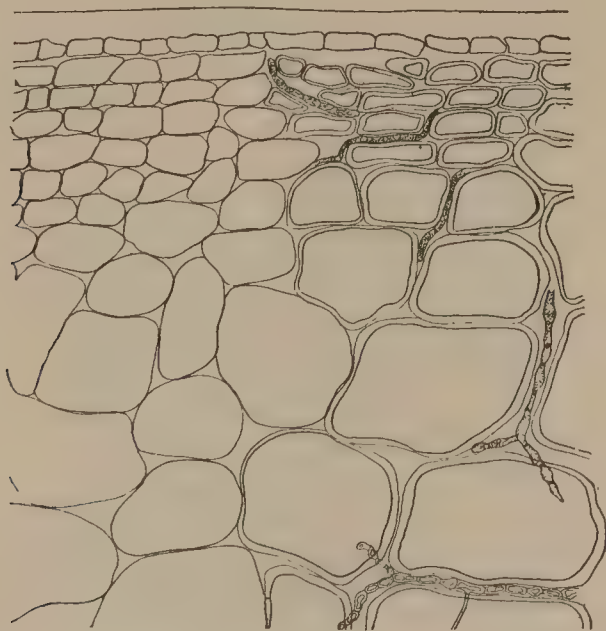


FIG. 173.—*P. cydoniæ*. Histological changes in the fruit of apple. Healthy tissue at left, diseased at right. After Hesler.

usually continuous, occasionally 1 or even 3-septate. Mycelium hyaline when young, brown when old.

On apple, pear, hawthorn, quince, crab apple, peach, witch hazel, oak, on fruit leaves and branches.



FIG. 174.—Pycnidium of *P. cydoniæ*.
After Hesler.



FIG. 175.—Asci and paraphyses
of *P. cydoniæ*. After Hesler.

The fungus winters as mycelium in the host tissues and as pycnospores in pycnidia. New infections are by pycnospores and usually through wounds. The species appears to consist of many biologic races.

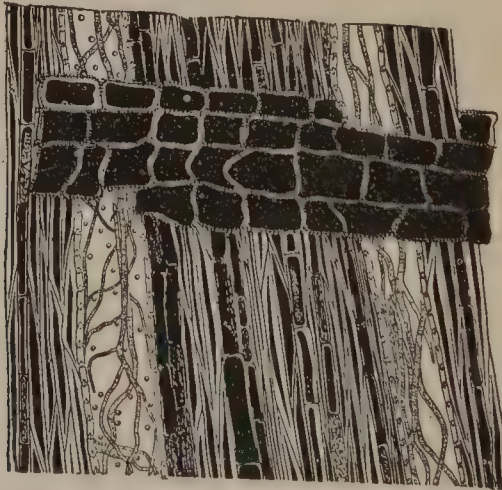


FIG. 176.—*P. cydoniæ*, longitudinal section of a part of
apple twig, showing brown deposit in woody elements
and mycelium in the xylem ducts. After Hesler.

The mycelium is usually intercellular and in fruit is found in advance of the pathological color changes that it causes. In

the leaves hyperplasia of the palisade and the spongy tissue results. In the wood the mycelium is found in the ducts and wood parenchyma, and a brown deposit is made (Fig. 176). In superficial bark cankers a protective cork layer (Fig. 177) develops below the invaded region.

Other species are on willow, strawberry, birch, chestnut, oak, fir, mulberry, elm, magnolia.

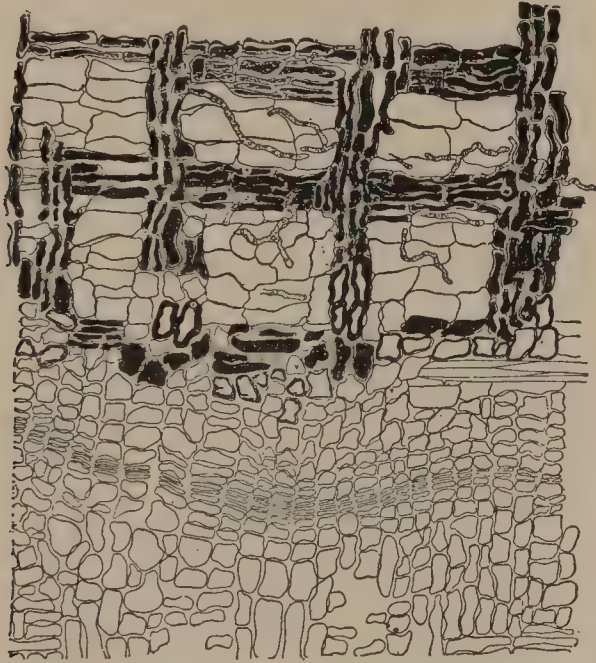


FIG. 177.—*P. cydoniæ*, showing brown deposit in medullary ray cells and phloem parenchyma. Below the diseased region is seen the cork layer. After Hesler.

Venturia Cesati & de Notaris (p. 178)

Perithecia superficial or erumpent, bristly, ostiolate, membranous, dark colored; asci sessile or short stipitate, ovate or saccate; spores oblong to ovoid elliptic, hyaline or yellowish; paraphyses usually none.

The conidial stages in some cases belong to the form genus *Fusicladium* and constitute the parasitic portion of the life history of the fungus, the ascigerous form usually being limited to old or wintered parts of the host.

V. pirina Aderh.

Perithecia gregarious, smooth or bristly, globose, 120–160 μ ; asci cylindric; spores unequally 2-celled, yellowish-green, 14–20 x 5–8 μ .

Conidia (= *Fusicladium pirinum*) effused, velvety, blackish-olive, conidiophores short, wavy or knotted, thick-walled; conidia ovate fusoid, olive, becoming 1-septate with age, 28–30 x 7–9 μ .

It is found on the pear wintering in perithecial form on leaves, and in conidial form, or as mycelium on twigs.



FIG. 178.—Mature perithecium of *V. inaequalis*, showing mature ascospores, the method of ejection of ascospores, and the bristles that sometimes occur about the ostiole. After Wallace.

V. inaequalis (Cke.) Wint. (= *V. pomi* [Fries] Winter)

Perithecia globose, short-necked, 90–160 μ , smooth or bristly above; asci cylindric, 55–75 x 6–12 μ , without paraphyses, 8-spored; spores yellowish-green, unequally 2-celled, upper cell shorter and broader, 11–15 x 5 μ .

Conidia (= *Fusicladium dendriticum*) effused, velvety, forming dendritic patches of compact masses of erect closely septate, brown mycelium; conidiophores closely septate, brown, 50–60 x 4–6 μ , wavy or nodulose; conidia solitary, terminal, obclavate, yellowish-olive, continuous when young but at length septate, 12–22 x 6–9 μ .

Its hosts are apple and other pomaceous fruits except the pear.

The two conidial forms have been long regarded as identical and are found in literature as *Fusicladium dendriticum*. The olive-green mycelium in both cases grows subepidermally in the leaf and fruit, killing the epidermis and forming subepidermal stromata from which conidiophores are produced. Stromatal development is also said often to be subcuticular, resulting in a separation of the cuticle from the epidermis.



FIG. 179.—*V. inaequalis*. A, portion of a section through a scab spot on apple; b, spreading under and lifting the cuticle, a; c, partly disorganized cells of the apple; e, healthy cells of the apple. B, two conidiophores with summer spores f. C, spores germinating. After Longyear.

The conidia are produced apically on short stalks and as each conidium is cut off the conidiophore grows forward, leaving scars equal in number to the conidia produced.

Perithecia first form on the lower leaf surface in October and mature in April. They are most abundant when protected by sod or piles of leaves, and appear as small black pustules often on grayish spots. Their connection with the conidial stage was first shown by Aderhold and confirmed by Clinton.

Cultures from ascospores gave rise to typical conidia.

Other species are found on hawthorn, cherry, birch, aspen and sorbus.

Didymellina v. Höhn. (p. 178)

Perithecia covered, membranous, globose-depressed, minutely papillate, black; asci cylindric or clavate; spores ellipsoid or ovate, 2-celled, hyaline; paraphyses none. Like *Didymella* except lacking paraphyses.

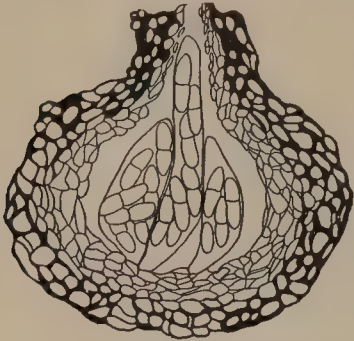


FIG. 180.—*D. iridis*; perithecium showing asci and spores. After Tisdale.

D. iridis. (Desm.) v. Höhn.

Perithecia scattered, smooth, globose, dark, 130–246 μ , subepidermal, ostiole papillate; asci 36–54 x 72–117 μ , no paraphyses; spores oval or elliptical, 1-septate, constricted, 10–16 x 30–54 μ . Conidia (= *Heterosporium gracile* Sacc.). Conidiophores olivaceous, crooked, 11–150 μ ; conidia echinulate, cylindrical, ends

rounded, 2 to 3-septate, 14–19 x 40–60 μ .

It causes a spot on the iris leaves.

Didymosphæria Fuckel (p. 178)

Perithecia immersed, later erumpent; asci cylindric to clavate, 8-spored; spores elliptical to ovate, 2-celled, brown.

This genus differs from *Didymella* chiefly in the dark-colored spores. It contains some one hundred twenty species and has occasional parasitic representatives on leaves and twigs.

D. catalpæ Parker

Perithecia very small, scattered, embedded in the tissue of the leaf, pyriform to nearly spherical, varying in width from 48–104 μ , and in depth from 64–140 μ ; ostiole broadly conical, erumpent; asci 8-spored, cylindrical, usually somewhat curved; paraphyses few or wanting; spores oblong-elliptical, hyaline or yellowish, uniseptate, constricted in the middle, 9.6–13 x 3–4 μ . On *Catalpa*.



FIG. 181.—*Didymosphæria*. C, an ascus; D, conidiophore and conidia. After Brefeld.

Leptosphæria Cesati & de Notaris (p. 178)

Perithecia at first subepidermal, at last more or less erumpent, subglobose to globose, coriaceous-membranous, ostiole usually papil-

late; asci subcylindric; spores ovoid, oblong or fusoid, two or more septate, olivaceous, yellowish or brown.

There are about five hundred species, many of which in the conidial forms embrace *Cercospora*, *Phoma*, *Hendersonia*, *Sporodesmium*, *Septoria*, *Coniothyrium* or *Cladosporium*.

L. coniothyrium (Fel.) Sacc.

Perithecia gregarious, subepidermal, depressed, globose, black; ostiole papillate, erumpent; asci cylindric, stipitate, 8-spored, $66-96 \times 4-6 \mu$; spores 1-rowed, oblong, 3-septate, constricted, fuscous, $10-15 \times 3.5-4 \mu$.

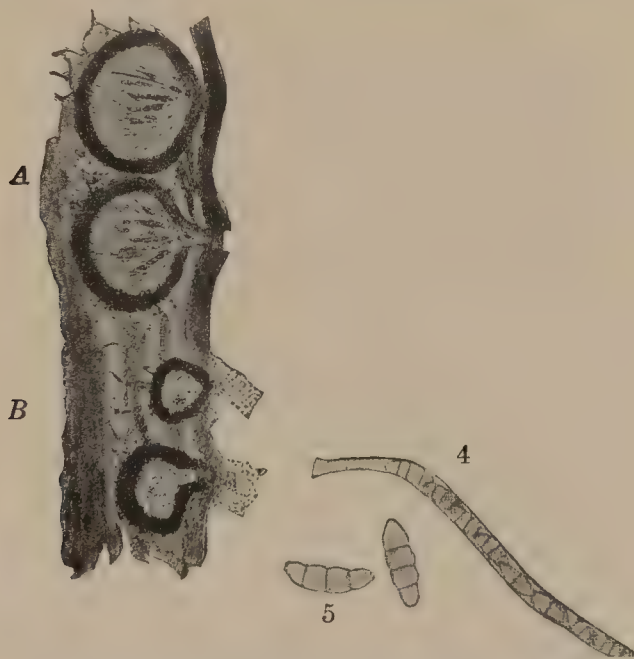


FIG. 182.—Cross-section of raspberry bark showing two perithecia of *L. coniothyrium* at the top, *A*, and two pycnidia of *Coniothyrium fuckelii*, at the bottom, *B*. 4. An ascus of *L. coniothyrium*. 5. Spores of *L. coniothyrium*. After Stewart.

Pycnidia (= *Coniothyrium fuckelii*) superficial, scattered, dark, $180-200 \mu$, globose-depressed; conidia numerous, globose to short-elliptic, $2.4-5 \times 2-3.5 \mu$.

It occurs on black and red raspberries causing cane-blight; also as the cause of rose and apple canker and apple fruit rot.

L. avenaria Weber.¹

Conidia (= *Septoria avenae* Frank.)

Pycnidia more or less scattered, often in rows, subepidermal,

¹ Weber, George F. *Septoria diseases of cereals*, *Phytop.* **12**: 10, 449, 1922.

globose to subglobose, 90–150 μ in diameter, ostiole slightly elevated, 20–30 μ in diameter; spores rod-shaped, 3-septate when mature, hyaline, 3–4 x 25–45 μ ; perithecia globose to subglobose, 60–130 μ in diameter; ostiole usually round, not protruding, 12–20 μ in diameter; asci narrowly clavate with rounded tips, hyaline, thin walled, 10–18 x 30–100 μ ; asci 8-spored; ascospores fusoid; 3-septate, constricted, light yellow to slightly olivaceous, 4.5–6 x 23–38 μ ; paraphyses cylindrical, hyaline, 2 x 60 μ . On oats.

L. tritici (Gar.) Pass.

Perithecia innate, globose, black, papillate; asci clavate, short-stipitate, 8-spored; paraphyses filiform, 48–50 x 15–16 μ ; spores 2-seriate, round, fusoid, 3-septate, constricted, pale, 18–19 x 4.2–5.5. μ .

Conidia (=Ascochyta graminicola). Pycnidiospores usually 2-celled, 12–20 x 3.5 μ . On wheat.

Others are on grape, rye, sugar cane, rice, rape, clover, alfalfa, potato, beet, phlox, rhododendron.

Ophiobolus Riess (p. 178)



FIG. 183.—Asci and spores of *O. cariceti*, on wheat. After Fitzpatrick, Thomas and Kirby.

Perithecia scattered, subglobose, submembranous, covered or sub-erumpent, ostiole papillate or elongate; asci cylindric; spores fusiform, hyaline or yellowish.

A genus of some one hundred twenty-five species.

O. cariceti (B. & Br.) Sacc.^{1, 2}

O. graminis Sacc.

Parasitic on wheat, barley, rye and various wild grasses, causing the take-all disease. The mycelium permeates the roots of the host causing them to become brittle and easily broken away and develops profusely above the crown of the plant in and about the leaf sheaths. It forms a definite, thick plate between the inner

leaf sheath and the culm; the mycelial plate usually adhering to

¹ Kirby, R. S. The take-all disease of cereals and grasses. *Phytop.* **12**: 66, 1922.

² Fitzpatrick, H. M., Thomas, H. E., Kirby, R. S. The *Ophiobolus* causing take-all of wheat. *Mycol.* **14**: 30, 1922.

the culm when the leaf sheaths are stripped away, composed of coarse, dark-brown hyphæ, 3–6 μ in diameter, which frequently run parallel to one another forming broad, flat, ribbon-like strands resembling somewhat compressed rhizomorphs; perithecia membranaceo-carbonaceous, dark-brown to black, smooth, rostrate, ostiolate, occurring on the roots of the host, singly or in groups, the individuals in a group occasionally fused laterally but no true stromatic tissue developed, often developed in great numbers, when young hidden from view but, at maturity the beaks protruding



FIG. 184.—*O. cariceti*, portion of the mycelial plate formed around the culm. After Fitzpatrick *et al.*

and prominent. The obliquely attached curved beak is so characteristic of the species as to be almost diagnostic. Ascigerous portion of the perithecium globose or subglobose, 330–500 μ in diameter, narrowing gradually into the truncate-conoid to cylindrical beak; asci numerous, fascicled, elongate-clavate, straight or curved, short-stipitate to sessile, 90–115 x 10–13 μ , rounded at the apex, 8-spored, thin-walled; paraphyses abundant, thread-like, flexuous, unbranched, hyaline; ascospores hyaline to faintly yellowish in mass, linear, curved, broader at the middle and tapering gradually toward the ends, the upper end rounded, the basal end more acute, 60–90 x 3 μ , when young, continuous and multiguttulate, at matur-

ity 5 to 7-septate, not reaching morphological maturity until late autumn or winter.

Inoculations with pure cultures have produced the typical take-all disease on wheat, barley, rye and members of eight other grass genera. Mature perithecia were found about ten weeks after inoculation.

Pleospora Rabenhorst (p. 178)

Perithecia covered at first, later more or less erumpent, usually membranous, black, globose; asci oblong to clavate; spores elongate or ovate, muriform; paraphyses present.

Conidia occur as *Macrosporium*, *Alternaria*, *Cladosporium*, *Sporodesmium*, *Phoma*, *Helminthosporium*.

There are over two hundred twenty-five species, mostly saprophytic. Many conidial forms whose connection to this genus have not yet been definitely proved probably belong to it and are in many instances parasites.

P. tropeoli Hals. is reported as the cause of disease of the cultivated *Nasturtium*.

Perithecia pyriform, 140–160 μ ; asci oval, one-sided, spores hyaline or very light-olivaceous, 25–35 \times 6–8 μ .

The *Alternaria* form was grown from the ascospores by Halsted and from the

Alternaria spores, grown in pure culture, perithecia were obtained in about twelve days.

Others are on orange, chicory, pea, tobacco, rice, carrot, elm, box-elder, hyacinth.

Pleosporæ on grains.

Several species of *Pleospora* with their attendant conidial forms of *Helminthosporium* and *Alternaria* are known on various grains and grasses. Cross inoculation experiments have shown here biologic specialization similar to that encountered among the *Erysipheæ*, in that conidia or ascospores from one host usually give negative results on host species other than that on which they grew. Thus Diedicke says the *Pleospora* of *Bromus* cannot be grown on *Triticum repens* nor on cultivated barley or oats. *Helminthosporium* was formerly thought to be the conidial stage

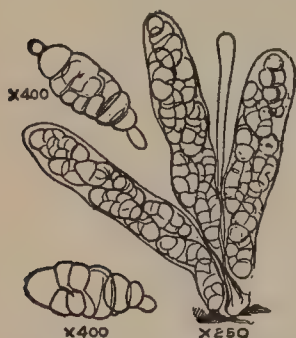


FIG. 185.—*Pleospora* from passion-fruit. The spores are just beginning to germinate, the end cells starting first. After Cobb.

of all of these grain Pleosporas, but recent work of Diedicke shows that one form which he regards as *P. trichostoma* (Fr.) Wint. possesses an *Alternaria* conidial form. Following Diedicke, the forms given below would be recognized. The discussion of the conidial forms is given on page 404.

***P. bromi* Died.**

Perithecia brown; hairy; asci 189–288 x 34–59 μ , saccate, thin-walled; spores 2-seriate, golden-brown, 4-celled, 48–83 x 19–33 μ .

Conidia (= *Helminthosporium bromi*) on brownish spots, 108–150 x 13–20 μ , 5 to 7-celled, dark colored. On *Bromus*.

***P. gramineum* Died.**

Conidia (= *Helminthosporium gramineum*); conidiophores short, subflexuose, light-brown; conidia solitary, elongate-cylindric, 4 to 7-celled, 15–19 μ wide and of variable length.

On barley and rye.

***P. tritici-repentis* Died.** is found on *Triticum repens*. (Conidia = *Helminthosporium tritici-repentis*.)

***P. trichostoma* (Fr.) Wint.** (= *Pyrenophora trichostoma* (Fr.) Sacc.)

Perithecia gregarious, innate, conical, black, ostiole surrounded by black hairs, which are simple, septate, 6–8 μ in circumference; asci clavate, 300 x 40 μ ; spores broadly oblong, obtuse, unequally 4 to 6-septate, muriform, brownish, 52 x 20 μ ; paraphyses branched.

On rye with the conidial form = *Alternaria trichostoma* Died.

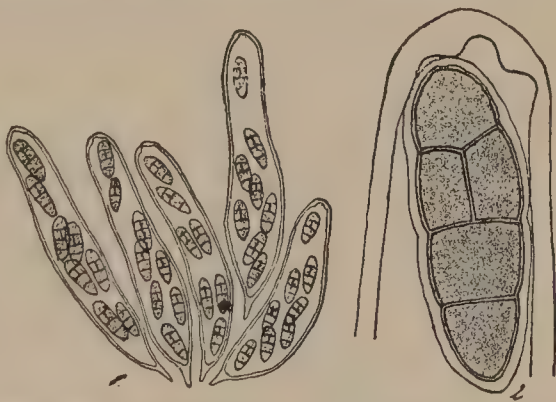


FIG. 186.—*P. trichostoma*. 1, group of asci, 2, a single spore at the apex of an ascus. After Diedicke.

Gnomoniaceæ (p. 158)

Perithecia sunken, with an elongate, cylindric, beak-like ostiole, rarely with a papillate one; leathery or membranous, rarely borne on a stroma; asci mostly thickened apically and opening by a pore; spores hyaline; paraphyses usually absent.

A family of over one hundred fifty species; two genera contain important pathogens.

KEY TO GENERA OF *Gnomoniaceæ*

- Spores 1-celled, mouth of the perithecium
 elongate, beak-like, straight; asci 8-spored;
 spores ellipsoid or fusoid; stroma present. . . 1. *Glomerella*, p. 190.
 Spores 2 or more-celled; asci 8-spored; spores
 elongate, 2 to 4-celled. 2. *Gnomonia*, p. 196.

Glomerella Spaulding & von Schrenk ¹

Perithecia cespitose, membranous, dark brown, rostrate, of a lighter color at the apex in early stages, flask-shaped, hairy, on or immersed in a stroma; asci sessile, clavate; spores 8, hyaline, oblong, 1-celled, slightly curved or straight, elliptic; paraphyses usually none. Conidia in part = *Colletotrichum* and *Gloeosporium*, a genetic connection first proved by Atkinson in 1898.

This genus was first described by Stoneman, from perithecia obtained from cultures of the conidia, as *Gnomoniopsis*. On account of preoccupation it was renamed *Glomerella* by Spaulding and von Schrenk in 1903.

Studies by Shear have shown that there is much variation in pure line cultures both from ascospores and from conidiospores. This leads to great uncertainty as to specific limitations. The conidial forms are very common and are usually parasitic. The ascigerous stages are comparatively rare. Sometimes they are found in nature; again only in artificial culture.

Some forms known to be ascigerous may in one culture yield abundant perithecia while other cultures of the same fungus may persistently refuse to bear asci at all.

G. cingulata (Stonem) S. & v. S. As the cause of the bitter rot of apples this fungus may be described as follows.

Perithecia on decaying fruits, subspherical, more or less grouped;

¹Shear, C. L. and Wood, A. K. Studies of fungous parasites belonging to the genus *Glomerella*. U. S. Dept. Agr. Bur. Pl. Ind. Bul. 253, 1913.

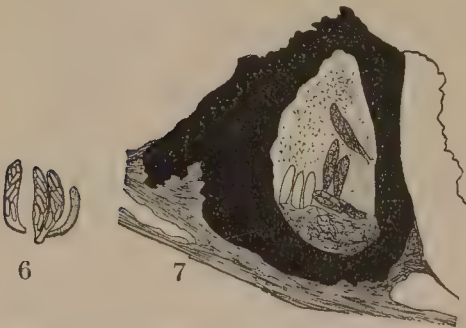


FIG. 187.—7, Perithecium of *G. cingulata* showing asci *in situ*; 6, asci showing detail. After Spaulding and von Schrenk.

asci subclavate, fugaceous, 55–70 μ ; ascospores allantoid, 12–22 x 3–5 μ ; conidial stage with small sori, developing in more or less concentric circles, usually soon rupturing and pushing out spores in small pinkish masses; spores hyaline to greenish, chiefly oblong, unicellular 10–28 x 3.5–7 μ .

The conidial stage of this fungus was first described by Rev. M. J. Berkeley in 1854 as a *Septoria*. It was later transferred to the form genus *Gloeosporium*. The ascigerous stage was found by Clinton in 1902.

The conidia germinating on apples send germ tubes through the skin, usually through wounds, occasionally through a sound surface. The mycelium grows subepidermally, branching rapidly, intercellularly and intracellularly, absorbing the sugar and other nutrients present, and resulting in brown discoloration of cells and dissolution of their connection with neighboring cells. The mycelium is first hyaline but later, especially in the stromata, it may be quite dark. Acervuli soon appear, often in concentric rings, lifting the epidermis with their palisades of conidiophores. The latter, at first hyaline, later olivaceous, bear the numerous conidia, which are pinkish, rarely cream-colored, in mass. In germination the conidia become unisepate and often on the tips of the young mycelium develop the dark thick-walled irregular shaped spore-like structures, so common on the sporelings of the *Melanconiales*, which serve as organs of attachment to aid in infection.

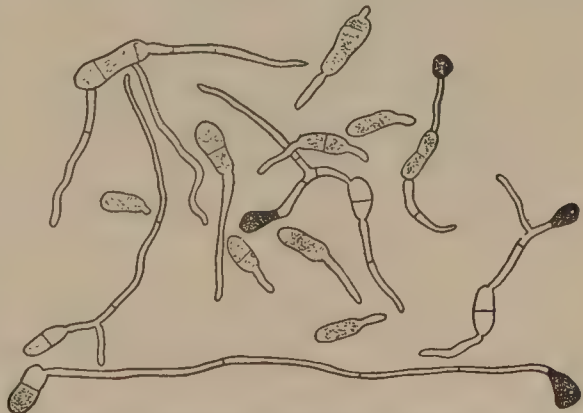


FIG. 188.—*G. cingulata*, germinating conidia. Note septa and appressoria. After Spaulding and von Schrenk.

Perithecia, which are often 4–5 mm. in diameter varying from one to many in each such stroma, appear in black knotted masses of mycelium. The asci were evanescent, disappearing soon after the spores mature.

Perithecia, which are often 4–5 mm. in diameter varying from one to many in each such stroma, appear in black knotted masses of mycelium. The asci were evanescent, disappearing soon after the spores mature.

In canker formation the mycelium grows in the live bark, killing it and the cambium. The cankers are thought to be comparatively short lived, perhaps surviving only the third year. Recipro-

cal inoculations between fruit and twigs have proved the fungus in the two cases to be identical. Conidia and ascospores develop on both fruit and twigs.

The mycelium hibernates in limb cankers and in mummified fruit. The fungus produces amylase, invertase, cytase and inulase acting on carbohydrates, also emulsin, lipolytic enzymes, protease, erepsin, and amidase.

From extensive cultural studies of both conidial and ascigerous material and trials by cross inoculation Shear and Wood conclude that this species is indistinguishable from fungi described under other names as follows:

Glomerella psidii (Del.) Shel. on guava.

Glomerella rubicola (Stonem.) S. & v. S. on Rubus.

Glomerella rufomaculans (Berk.) S. & v. S. on apple.

Colletotrichum camelliæ Mass. on Camellia and tea.

Colletotrichum carica Stev. and Hall on fig.

Colletotrichum glæosporioides Penz. on sweet orange and pomelo.

Colletotrichum theobromicolum Del. on Theobroma.

Glæosporium cingulatum Atk. on privet.

Glæosporium fructigenum Berk. on apple.

Glæosporium ribicolum E. & E. on Ribes.

Glæosporium rubi E. & E. on Rubus.

Glæosporium ruformaculans (Berk.) Thüm. on Vitis.

Læstadia camelliæ (Cke.) Berl. & Vogl. on tea.

Neozimmermannia elasticæ (Zimm.) Koord. on rubber plant, and that it also parasitizes quince, loquat, mango, avocado, coffee, palm, sweet pea, arrowroot, ginkgo, Gleditschia, Carya and other hosts, at least 34 all told.

Varieties of the species have been described on cranberries and cyclamen.



FIG. 189.—Plate culture of *G. cingulata* showing perithecia-bearing masses. After Spaulding and von Schrenk.

G. lindemuthianum Shear.¹=*Colletotrichum lindemuthianum* (Sacc. & Magn.) Bri. & Cav.

Perithecia as in *G. cingulata*. Spots subelliptic to irregular, depressed, brownish; acervuli scattered, surrounded by a few not very conspicuous black setæ; conidia oblong, ends rounded, straight or curved, $13-32 \times 3.5-5.3 \mu$; conidiophores cylindric, simple, $45-55 \mu$.

On the bean it attacks stems, leaves, cotyledons, or the pods, producing sunken spots of dead tissue which bear the numerous

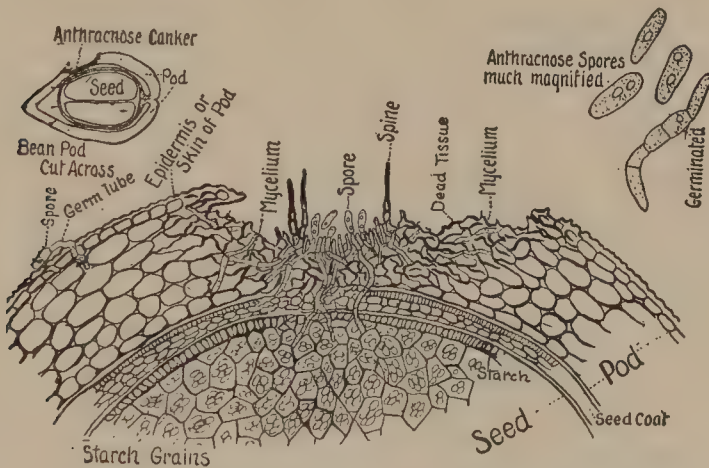


FIG. 190.—*C. lindemuthianum*. Showing relation of the fungus to the tissues of the bean. To the left above is a diagram of a section across a bean pod through a canker. The drawing below is a much enlarged largely diagrammatic view of a portion of this same section. It shows how the mycelial threads of the fungus may penetrate the seed coat and enter the starchy tissue of the seed, there to remain dormant until the following season. On the left is a spore germinating and penetrating the epidermis. To the right a magnified view of spores, one germinated. After Whetzel.

pink acervuli. The fungus enters the host through the cuticle by an invading hypha produced by an appressorium. Once within the host cell it penetrates into other cells. The protoplasm of invaded cells is killed and turns brown soon after being attacked. As the host cells collapse the mycelium develops to form a stroma, the base of the acervulus. Perithecia have been seen only in pure cultures. It has been shown that the mycelium on the fruit may penetrate through the pericarp and into the seeds beneath and there hibernate. Biologic specialization within the species has been shown to exist.

¹ Barrus, M. F. Bean anthracnose. Cornell Agr. Exp. Sta. Mem. 42, 1921.

Colletotrichum lagenarium (Pers.) E. & H. on fruit, leaves and stems of cucumbers, watermelons, squash, pumpkins and citron and *C. oligochaetum* on cucurbits, are possibly identical with *G. lindemuthianum*.

***G. piperata* (E. & E.) S. & v. S.**

Perithecia cespitose, thinly membranous, dark-brown, pyriform, hairy; asci clavate; spores slightly curved, elliptic, $12-18 \times 4-6 \mu$. Conidia (= *Gloeosporium piperatum*) on circular or oval spots; acervuli pustular, concentrically arranged, conidia $12-23 \times 5-6 \mu$.

The ascigerous stage was grown from pure cultures of the conidia taken from pepper by Miss Stoneman, the perithecia appearing



FIG. 191.—*G. piperata*, 99, perithecium external and in section.
100, asci in detail. After Stoneman.

about a month after inoculation. Typical conidia were also secured from ascospore sowings. It is possible that this is identical with *G. cingulata*.

***G. gossypii* (South.) Edg.**

Perithecia distinct or crowded, very abundant, covered, dark brown to black, subglobose to pyriform, $80-120 \times 100-160 \mu$, beak up to 60μ long; asci numerous, clavate, $55-70 \times 10-14 \mu$;

spores elliptic, hyaline, rarely curved, $12-20 \times 5-8 \mu$; paraphyses long and slender, very abundant.

Conidia (= *Colletotrichum gossypii*), acervuli erumpent, conidiophores colorless, longer than the spores, $12-28 \times 5 \mu$; conidia irregularly oblong, hyaline or flesh-colored in mass; setæ single or tufted, dark at base, colorless above, straight, rarely branched.

The conidial stage of this fungus was described by Southworth and independently by Atkinson on cotton.

The ascigerous stage was first seen by Shear & Wood in artificial culture.

The mycelium is richly branched and septate, usually hyaline but sometimes slightly smoky. It grows between and in the host cells which are often filled with it, causing loss of chlorophyll, browning and collapse. Studies by Atkinson and by Barre show that in case of diseased bolls the mycelium may extend through the pericarp, sporing on its inner wall; extend thence to the seeds; penetrate and grow in them, Fig. 192, and in the cells of the lint. Barre has shown that even the endosperm and cotyledons may be invaded, Fig. 192, and spores produced upon them while within the seed coats. Such seeds and lint may appear outwardly as though perfectly normal.

The conidia are formed in acervuli, subtended by stromata. Setæ, from few to many increasing with age of the acervulus, are present and conidia are occasionally found on them. In germination conidia usually develop one, sometimes two septa and produce dark chlamydo-spores. Acervuli are common on bolls, less so and smaller on leaves and stems.

The perithecia as found in the field by Edgerton in Louisiana were usually entirely embedded, with the beaks only protruding and were often numerous and crowded.

The fungus has repeatedly been studied in pure culture and numerous inoculations have thoroughly proved its pathogenicity, the disease usually showing within a few days after inoculation, though sometimes incubation is delayed much longer.

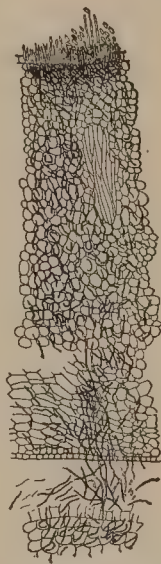


FIG. 192.—*G. gossypii*. Section of young boll, showing the fungus penetrating the hull and entering the young seed. Spores are being produced upon the outer portion of the hull and upon the surface of the young seed coat. After Barre.

Infection of stems is often at a wound such as a leaf scar; or on leaves at some point of weakness. Cotyledons and young plants are especially susceptible. On bolls infection is common at the line of dehiscence of the carpels. According to Barre, there is evidence that the fungus may destroy the contents of the boll before it shows upon the outside.

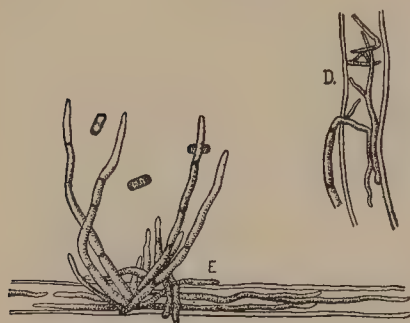


FIG. 193.—*G. gossypii*, D, and E, fungus growing in cotton lint fibers. After Barre.

Atkinson found that conidia five months old were alive, but that at seven months they failed to germinate.

Seed from a field that bore 35% infected bolls gave on germination, 12% of infected seedlings, the disease appearing upon cotyledons or hypocotyls even before they unfolded.

Gnomonia Cesati & de Notaris (p. 190)

Perithecia covered or erumpent, submembranous, glabrous, ostiole more or less elongate; asci ellipsoid or fusoid, apically thickened, opening by a pore; spores elongate, hyaline, 2 to 4-celled; paraphyses none.

There are some sixty species. *Fusicoccum*, *Myxosporium*, *Sporonema*, *Gloeosporium*, *Marssonina*, *Asteroma*, *Leptothyrium* occur in some species as the conidial form. The ascigerous form usually follows as a saprophyte after the parasitic conidial stage.

G. veneta (Sacc. & Speg.) Kleb.

Perithecia immersed, subglobose or slightly flattened, 150–200 μ , short, rostrate; asci long-clavate, 48–60 x 12–15 μ , generally bent at right angles at the base, apically very thick, opening by a pore; spores 14–19 x 4–5 μ , straight or slightly curved, unequally 2-celled, the upper cell longer.

Conidia variable in habitat and habit. (1) (= *Gloeosporium nervisequum*) acervuli subcuticular, 100–300 μ ; conidiophores short; conidia oozing out in a creamy-white mass, hyaline, ellipsoid, 10–14 x 4–6 μ , pointed at one end and rounded at the other. (2) (= *G. platani*) acervuli subepidermal, conidiophores long; conidia as above. (3) (= *Discula platani* = *Myxosporium valsoideum*) forming minute, subepidermal, erumpent pustules on

twigs; conidia elliptic to oblong, hyaline, $8-14 \times 4-6 \mu$; (4) (= *Sporonema platani* = *Fusicoccum veronense*). Pycnidia formed on old leaves on the ground, erumpent, subcuticular, brown, $200-300 \mu$; conidia numerous, oblong, ovoid to fusoid, $7-11 \times 3-4 \mu$.

The conidial form on sycamore and oak, first described in 1848, is common on leaves and young branches, the mycelium checking the sap-flow and causing death of surrounding tissue. A stroma



FIG. 194.—*G. veneta*, perithecium.
After Edgerton.



Fig. 195.—*G. veneta*, asci and spores. After Edgerton.

is formed on the outer layers of the mesophyll and from this arise the short conidiophores to constitute the acervulus.

The ascigerous form was first found by Klebahn on old leaves on which it matures about Christmas time.

Pure cultures from all the spore forms were compared by Edgerton confirming Klebahn's conclusion as to their identity. Cultures by Stoneman showed the forms on sycamore and oak to be the same.

***G. ulmea* (Schw.) Thüm.¹**

Perithecia subspherical, $250-300 \mu$ broad, $150-200 \mu$ deep, ostiole 100μ long, 75μ wide; asci 8-spored, paraphysate, oblong, $45-55 \times 9-11 \mu$; spores hyaline, unequally 2-celled, with a septum near the lower end, $8-10 \times 3-3.5 \mu$, small cell 2μ .

Conidia (= *Gloeosporium ulmeum* Miles). Acervuli somewhat gregarious, often confluent, borne on black stromata, usually over the base of the developing perithecium, covered by the darkened cuticle which later splits and cracks irregularly and finally breaks away entirely, subrotund or irregular, averaging 500μ in diameter, but often as large as 800μ , usually epiphyllous; conidiophores

¹ Miles, L. E. Leafspots of the elm. Bot. Gaz. **71**: 161, 1921.

cylindrical, crowded, $8-12 \times 1.5-2 \mu$, terminating in a threadlike projection on which the spores are borne; conidia elongate-oblong or cylindric, bacillar, pointed at one or both ends, straight or very slightly curved, hyaline, 1-celled, $8-10 \times 2-2.5 \mu$, when freshly collected extruded in small white masses.

The disease caused on various species of elm appears first in spring as small whitish or yellowish flecks on the upper side of the leaf soon after it unfolds. Black specks soon develop in this area

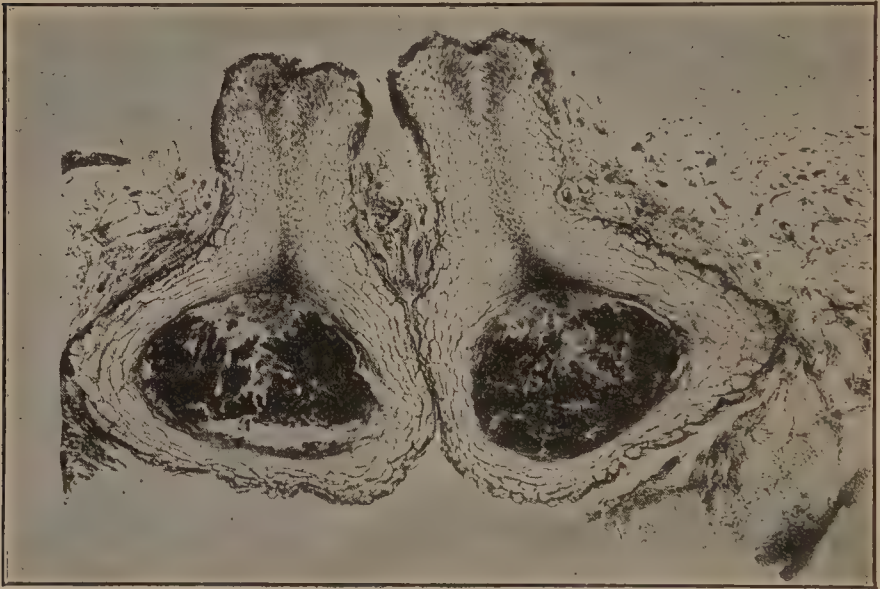


FIG. 196.—Two perithecia of *G. ulmea* in nearly mature condition. After Miles.

and by coalescence often form large (0.5–3 mm.), coal black spots, due to a stroma-like subcuticular structure. In June the perithecia here form, completing development in the following March. The connection between the conidial and ascigerous stages was demonstrated by inoculations.

***G. leptostyla* (Fr.) Ces. & d. Not.**

Perithecia conic, short-beaked; asci subclavate, $45-65 \times 10-12 \mu$; spores fusoid, curved, $18-22 \times 4 \mu$, hyaline. Conidial phase = *Marssonina juglandis*. Acervuli gregarious, hypophyllous, rounded; conidia obovoid, $8-10 \times 4-5 \mu$, 1-septate, pointed above, truncate below, greenish.

The connection between the conidial and ascigerous forms was demonstrated by Klebahn by pure cultures and by ascosporic

infection. The conidial form is common on walnut leaves, also especially severe on the butternut, often defoliating this host in midsummer.

Other species are recorded on cherry, blackberry, rice, oak.

Valsaceæ (p. 158)

Stroma effused, subglobose, conic or pulvinate, often indefinite; perithecia sunken in the stroma, scattered or clustered, black, leathery; asci cylindric or clavate; paraphyses usually present.

Over one thousand species, chiefly saprophytic. Conidia are present on hyphæ or in pycnidia.

KEY TO GENERA OF Valsaceæ

- | | |
|--|-------------------------------|
| Spores 1-celled, ellipsoid, with a hyaline membrane..... | 1. <i>Valsa</i> , p. 199. |
| Spores 2 to 4-celled, with cross walls only, hyaline, ellipsoid or fusoid..... | 2. <i>Diaporthe</i> , p. 200. |

Valsa Fries

Perithecia on a more or less definite stroma, immersed, the ostiole erumpent, black, firm; asci globose to cylindric, often long pedunculate; spores 1-celled, rarely 2-celled, cylindric, rounded hyaline or light-brown; paraphyses none.

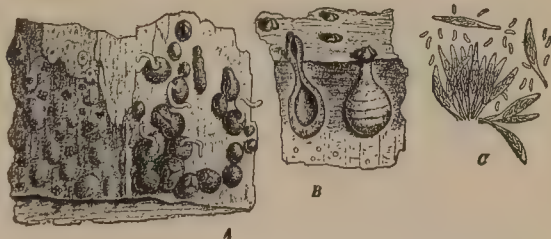


FIG. 197.—*Valsa*. A, habit sketch; B, perithecia; C, asci. After Tulasne.

V. leucostoma (Pers.) Fr.

Stroma strongly convex, 2–3 mm., whitish and granular within, outer layer coriaceous; perithecia immersed; asci fusoid-clavate, sessile, 35–45 x 7–8 μ ; spores biserial, allantoid, hyaline, slightly curved, 9–12 x 2–2.5 μ .

Conidia (= *Cytospora rubescens*); stromate, erumpent, reddish; conidia allantoid, 4 μ .

On pome and stone fruits causing "dieback" of twigs, and canker of limbs. On twigs infection often takes place through the buds. Diseased twigs show the mycelium matted in the cambium region.

Other species are on apple, plum, *Ficus*, cacao, *Alnus*, and *Hevea*.

Diaporthe Nitschke (p. 199)

Stroma variable, usually definite; perithecia membranous subcoriaceous, generally pale-cinereous within, with a cylindric or filiform beak; asci fusoid; spores fusoid to subelliptic, 2-celled, hyaline, appendaged or not; paraphyses none. Conidia=Phoma, Cytospora, etc.

D. taleola (Fr.) Sacc.

Stroma cortical, definite, depressed, pulvinate, 2-4 mm., covered; perithecia few, 4-10, buried, their ostioles converging, erumpent;

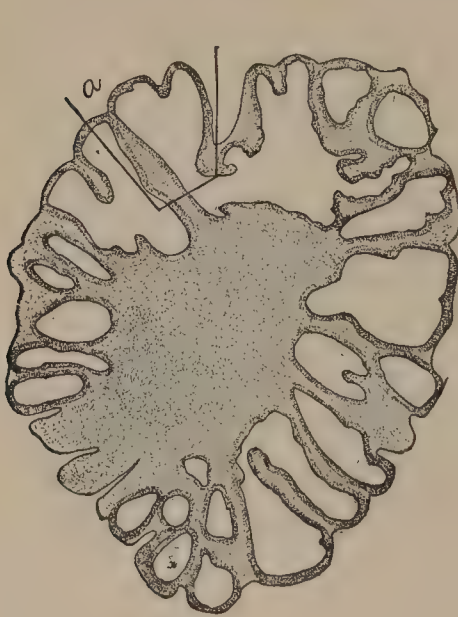


FIG. 198.—*Valsa leucostoma*. Cross-section of a pycnidium showing locules. After Stevens.

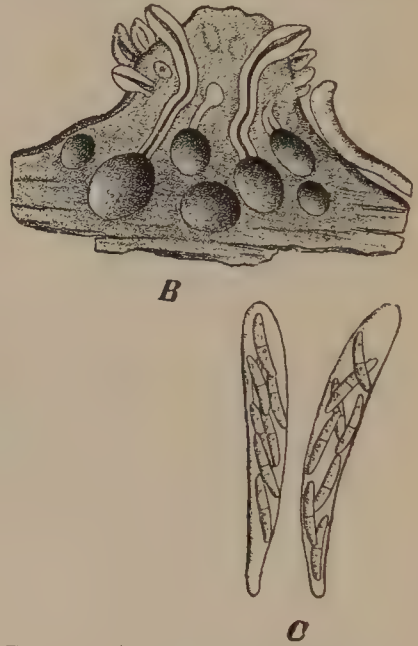


FIG. 199.—*Diaporthe*. B, stroma, in section; C, asci. After Tulasne.

pent in a small light-colored disk; asci cylindric, $120-140 \times 10-12 \mu$, spores elliptic, uniseptate, constricted, with setaceous appendages, $15-22 \times 8-9 \mu$.

It causes canker on oak, killing the cortex over large areas. A year later the cushion-like stromata appear. The mycelium penetrates both wood and bark, probably entering through wounds.

D. batatatis (E. & H.) Harter & Field.¹

Stromata valsoïd, immersed, erumpent, carbonaceous, with

¹ Harter, L. L. & Field, E. C. Sweet potato storage-rots. Jour. Agr. Res. **15**: 337, 1918.

exserted beaks 0.5–3 mm. long; perithecia 9–25, immersed, 120–370 μ broad; asci aparaphysate, 8-spored, 25–38 x 7–12 μ ; spores subelliptical, hyaline, 1-septate, constricted, 8–12 x 4–6 μ .

Pycnidia (= *Phoma batatae*) black, ostiolate, with irregular cavity; spores oblong-fusoid, 6–8 x 3–5 μ , continuous, hyaline; conidiophores filiform; stylospores in same or separate pycnidia.



FIG. 200.—*Cryptosporella viticola*. Fusicoccum stage from mummied grape. After Gregory.



FIG. 201.—*C. viticola* portion of a pycnidium showing conidiophores, conidia and scolecospores. After Shear.

In roots, stems and leaves of sweet potato. Ascigerous stage seen only in culture. The contents of the cells turn brown and the whole potato becomes dry and powdery.

***D. umbrina* Jenk.**

Pycnidia subglobose to lens-shaped; pycnosporos subfusoid, straight or slightly curved, hyaline, 5–11 x 2–3 μ ; sporophores simple or branched, tapering above, 12–40 μ in length; perithecia, two to five, immersed in a valsoid stroma, globose, with beak scarcely projecting above the epidermis, 110–290 μ in diameter; beaks 150–195 μ in length; asci clavate, subsessile, aparaphysate, 30–50 x 6–8 μ ; spores elliptical, usually hyaline, when mature sometimes light to olivaceous, continuous or sometimes with one pseudo-septum, 8–11 x 3–4 μ .

It forms cankers on the stems of cultivated roses.

D. phaseolarum (C. & E.) Sacc.¹ (= *Phoma subcircinata* E. & E.). Perithecia gregarious, 158–355 μ , buried, ostiole protruding; asci 28–46 x 58 μ , spores oblong-lanceolate, 6–12 x 2–4 μ ; pycnidia 158–475 μ in diameter; spores hyaline, oblong or fusoid, 1-celled, 6–9 x 2–4 μ ; stylospores present or absent, slender, hyaline, 12–31 x 1.5–2 μ .

This fungus causes spots in leaves, pods and stems of Lima beans. The life history and connection of the various morphological forms have been made from study of single-spore cultures. Wounds are not necessary to infection, the entrance being stomatal.

Other species of this genus are on pear, hop, dogwood, fir, rose.

Melanconidaceæ (p. 158)

A small family of about two hundred species.

Stroma pulvinate, sunken; perithecia sunken in the stroma, the mouth erumpent; asci cylindric or clavate; paraphyses present.

Cryptosporella Tulasne

Stroma valsoïd, pustuliform, covered; perithecia embedded,



Humphrey, det.

FIG. 202.—*C. anomala*. 31, stroma and perithecia; 32, an ascus; 33, spores. After Humphrey.



FIG. 203.—*Cryptosporella viticola*. Asci and paraphyses. After Shear.

subcircinate, with converging necks united in an erumpent disk; asci cylindric to globoid; spores elongate, cylindric, hyaline, 1-celled.

C. anomala (Pk.) Sacc.

Pustules prominent, 2–5 mm., erumpent; penetrating the wood

¹ Harter, L. L. Podblight of the Lima bean caused by *Diaporthe phaseolarum*. Jour. Agr. Res. 11: 473, 1917.

and generally having a thin, black crust beneath them, disk convex or slightly depressed, cinerous to black; perithecia black; crowded, deeply embedded in the stroma, often elongate, ostioles scattered, asci short, broad, fugaceous; spores 7–8 μ . hyaline, elliptic, simple.

On hazel and filbert causing the destruction of the tree tops.

C. viticola (Red.) Sh.

Pycnidia (=Fusicoccum) with labyrinthiform chambers, ostiolate but frequently rupturing. Spores hyaline, continuous, of two forms in the same cavity: 1. subfusoid, 7.5 x 2–5 μ ; 2. long, slender, curved, 18–30 x 1–1.5 μ ; perithecia buried in irregular pulvinate stromata, beak exserted; asci 60–72 x 7–8 μ ; paraphyses slender, septate, wavy; ascospores subelliptic, hyaline, continuous, 11–15 x 4–6 μ . Fig. 203.

The conidial stage was described by Reddick as the cause of necrosis of grape vines. The ascigerous form in pure culture in the hands of Shear gave rise to the typical conidial form, identical with that grown from pure cultures of the pycnosporos.

Calosphæria. Tulasne

Perithecia astromate, free or on the inner bark, scattered or clustered, ostiole more or less elongate; asci clavate, fasciculate; spores small, cylindric, curved, hyaline, continuous; paraphyses longer than the asci, stout lanceolate, evanescent.

C. princeps Tul.

Perithecia on the inner bark in orbicular or elliptic groups, generally densely crowded, globose, smooth and shining, necks long, decumbent, flexuose, cylindric, erumpent; asci 12–26 x 4 μ ; spores 5–6 x 1–5 μ .

On plum, cherry, peach and even pomaceous trees.

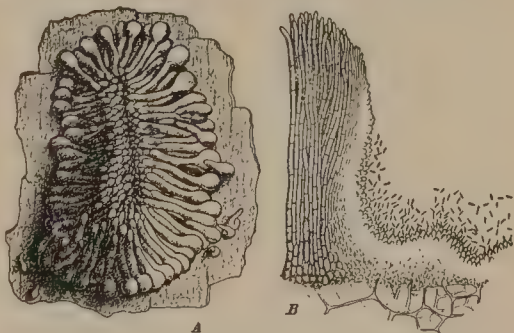


FIG. 204.—*Calosphæria princeps*. A, group of perithecia; B, conidial stroma. After Tulasne.

Melogrammataceæ (p. 158)

Stroma usually pulvinate, rarely effused, hemispheric, subperidial then erumpent and more or less superficial; perithecia sunken

in the stroma; conidia occur in acervuli on the surface of the young stromata or in pycnidia.

A family of over one hundred twenty-five species.

KEY TO GENERA OF *Melogrammataceæ*

Spores 1-celled, ellipsoid or ovate, asci clavate . . 1. *Botryosphæria*, p. 204.

Spores 2-celled, with cross walls only, hyaline;

paraphyses present; perithecia long-beaked . 2. *Endothia*, p. 205.

Botryosphæria Cesati & de Notaris

Stroma pulvinate, black, perithecia at first sunken in the stroma, remaining so or becoming more or less prominent, usually small, globose, ostiole inconspicuous, papilliform; asci clavate; spores elliptic to oval, hyaline, continuous; paraphyses present.

B. ribis G. & Dug. Stromata black, more or less pulvinate, outer surface botryose, 1–4 mm. in diameter, usually 2–3 mm.,

and surrounded by the fissured periderm, regularly scattered or in more or less definite, longitudinal rows or elongated stromata. Perithecia somewhat top-shaped, with papillate ostioles and usually projecting, sometimes practically superficial, few to many in a stroma and usually interspersed among pycnidia, 175–250 μ in width.

Asci clavate, 80–120 x 17–20 μ , and with numerous

filiform paraphyses. Spores fusoid, continuous, hyaline, 16–23 x 5–7 μ .

Pycnidia of the compound stylosporoc form, *Dothiorella*, are borne in the same or similar stromata; spores fusoid, continuous, hyaline, 18–31 x 4.5–8 μ . Pycnidia of the simple stylosporoc form, *Macrophoma*, are embedded in the outer bark under the much-raised primary cortex of young shoots, depressed globular, 175–250 μ wide; spores fusoid, hyaline, continuous, 16–25 x 4.5–7.5 μ .

The cause of a blight of canes of currants.



FIG. 205.—*Botryosphæria*. B, stroma in section; C, part of perithecium and pycnidium in section. After Tulasne.

Extensive inoculation experiments and pure culture studies have definitely established pathogenicity.

B. berengeriana de Not.

Stromata erumpent-superficial, pulvinate; asci 70–80 x 18 μ , paraphyses filiform; spores 20–25 x 10–12 μ , hyaline.

On pecan causing die-back of twigs and limbs.

B. fuliginosa (M. & N.) E. & E. is the cause of a minor disease of cotton bolls. A pycnidial stage of it is a *Macrophoma*. Pycnidia black, 110–200 x 120–140 μ ; spores 14–33 x 7–10 μ ; perithecia 190–360 x 250–320 μ ; ascospores 20–27 x 10–16 μ .

B. marconii (Cav.) Charles and Jenkins¹

Perithecia globose, perforate, 140–160 μ in diameter; conidiophores of the microconidia mostly dichotomously branched, septate, hyaline; microconidia polymorphic, ovate, elliptical, or terete, continuous, hyaline, 4–5.5 x 1.5–2 μ ; macroconidia fusiform or ellipsoid, continuous, hyaline, 16–18 x 5–6 μ ; conidiophores of macroconidia slender, generally 12–15 μ in length; asci clavate, 8-spored, 80–90 x 13–15 μ ; paraphyses filiform; spores fusoid, hyaline to pale green, 16–18 x 7–8 μ ; microconidia, macroconidia, and asci produced in the same perithecium. On hemp causing wilting and drooping of the leaves. The fungus also attacks the outer ends of the branches.

Endothia Fries (p. 204)

Stroma valsoid, covered, then erumpent; perithecia with long ostioles; asci 8-spored; spores 2-celled, hyaline.

¹ Charles, V. K. and Jenkins, A. E. A fungous disease of hemp. Jour. Agr. Res. 3: 81, 1914.

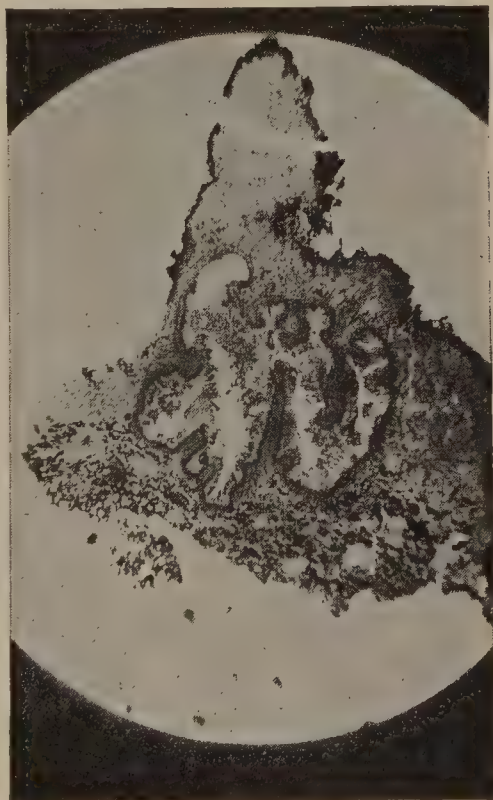


FIG. 206.—*E. parasitica*: section of a stroma showing perithecia with long ostioles. After Anderson and Rankin.

E. parasitica (Murr.) And. & And. Stromata orange, later reddish-brown, erumpent. On smooth bark 2.4 x 1.2 mm; on rough bark coalescing in the crevices to stromata several centimeters long; pycnidia on smooth bark, globose, solitary, astromate; conidiophores 20–40 x 1.5 μ , simple or branched; spores hyaline, sticky, issuing in cirri, 1.3 x 3.5 μ , oblong to cylindrical. Older pycnidia in stromata irregular or labyrinthiform; perithecia

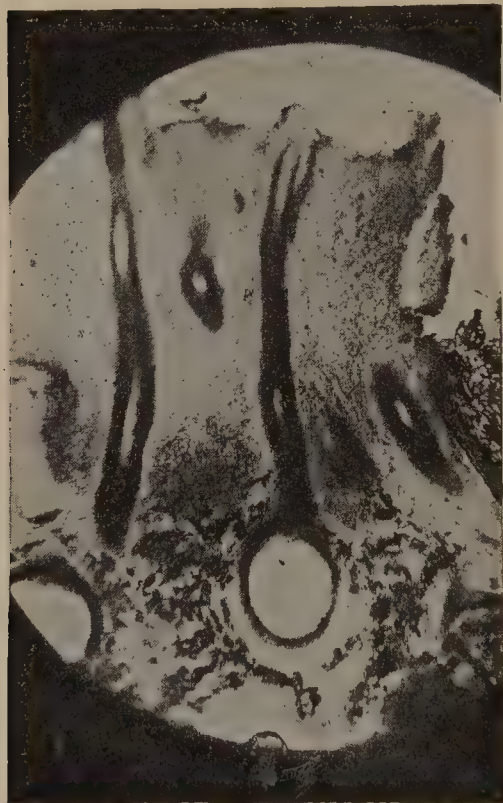


FIG. 207.—*E. parasitica*: section of a stroma showing pycnidium of irregular shape. After Anderson and Rankin.

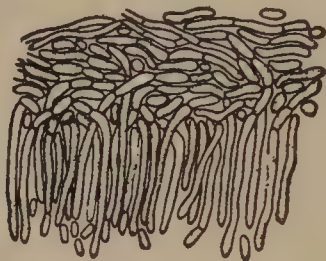


FIG. 208.—*E. parasitica*: section of wall of a pycnidium showing conidia and conidiophores. After Anderson & Rankin.



FIG. 209.—*E. parasitica*: asci and ascospores. After Anderson & Rankin.

12–40 in a stroma, 350–400 μ wide, deeply buried, with an ostiole of a length 4–6 times the diameter of the perithecium; asci 8-spored, average size 51 x 9 μ ; spores oblong to oval, 2-celled, constricted, 4.5 x 8.6 μ ; mycelium 1.5–12 μ thick, yellow, due to an alcohol-soluble pigment, forming fan-like mats in the diseased bark. Parasitic on chestnut causing bark cankers, and saprophytic on oak, sumac, maple, hickory. Inoculation by mycelium gives positive results

in about 2 weeks, spores 3–5 weeks, and it appears that a wound is necessary.

After attaining vigor on wounded cells the mycelium pushes *en masse*, not singly, into the living bark tissue. All walls of more or less pure cellulose, except medullary rays, are destroyed and replaced by mycelium. The destruction of various bark tissues is largely attributed to mechanical action.

Xylariaceæ (p. 158)

Stroma variable, usually free but often more or less sunken in the matrix, either upright and often branched or horizontal, effused, crustaceous, pulvinate, globose or hemispheric, black or becoming black, usually woody or carbonous; perithecia peripheral, immersed, leathery or carbonous, black; asci cylindric or cylindric-clavate, 8-spored; spores continuous, brown or black, fusiform or ellipsoid, paraphyses present or absent.

A family of over five hundred species.

KEY TO GENERA OF Xylariaceæ

- | | |
|--|--------------------------------|
| Stroma encrusted, shield-form, globose or hemispheric, without a sterile base; conidial layer beneath the surface of the stroma, erumpent..... | 1. Nummularia , p. 207. |
| Stroma erect, simple or branched, clavate or cylindric, with a sterile base..... | 2. Xylaria , p. 210. |

Nummularia Tulasne

Stroma orbicular, cupulate or discoid, becoming black, marginate; perithecia monostichous, peripheral, immersed; asci cylindric; spores subelliptic, continuous, dark.

N. discreta (Schw.) Tul.

Stroma erumpent, orbicular, 2–4 mm., cupulate, with a thick raised margin. Perithecia ovate, cylindric, nearly 1 mm. long, abruptly contracted above into a short neck; asci 8-spored, 110–180 x 10–15 μ ; spores subglobose, nearly hyaline, then opaque, 10–12 x 13–16 μ ; paraphyses filiform, short and branched. Conidiophores arise from the stromata; conidia oval, acute at base, 5 x 8 μ .

This fungus, usually a saprophyte, is a serious parasite on the apple.

The mycelium grows first in the wood attacking the parenchyma cells and medullary rays, proceeding to the bark after the underlying tissues have been killed. From July to September the stromata, 3-5 mm. in diameter, appear in the bark

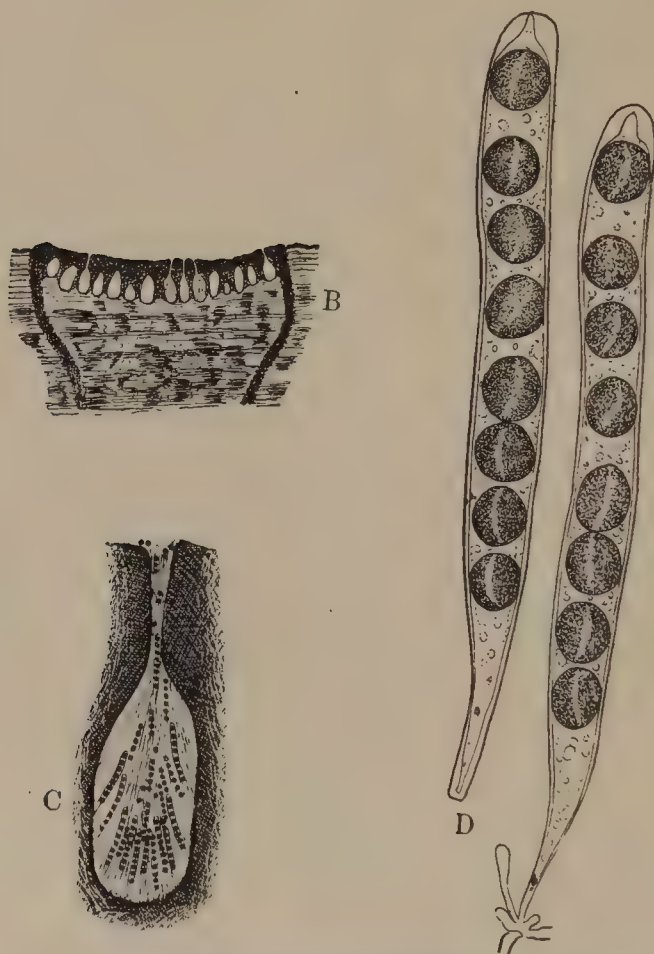


FIG. 210.—*N. discreta*, B, stroma and perithecia, C, a perithecium, D, asci. After Hasselbring.

and bear conidia in the fall or early spring. The perithecia develop during the second or succeeding years. Infection occurs only through wounds. In living tissue the mycelium advances chiefly through the ducts and medullary rays. Cells are killed several centimeters distant from the fungus. The mycelial advance is faster in old, e. g., 4-year old wood, than in younger wood.



FIG. 211.—*N. discreta*, section of a stroma with ascospores within and conidia on the surface. After Cooper.

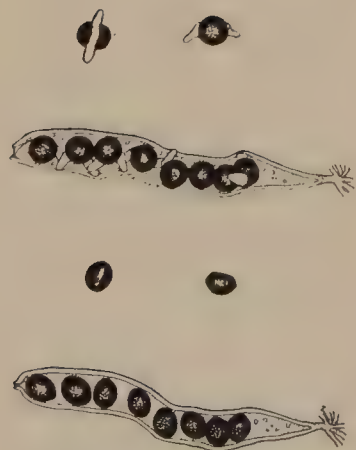


FIG. 212.—*N. discreta*, asci and ascospores. After Cooper.

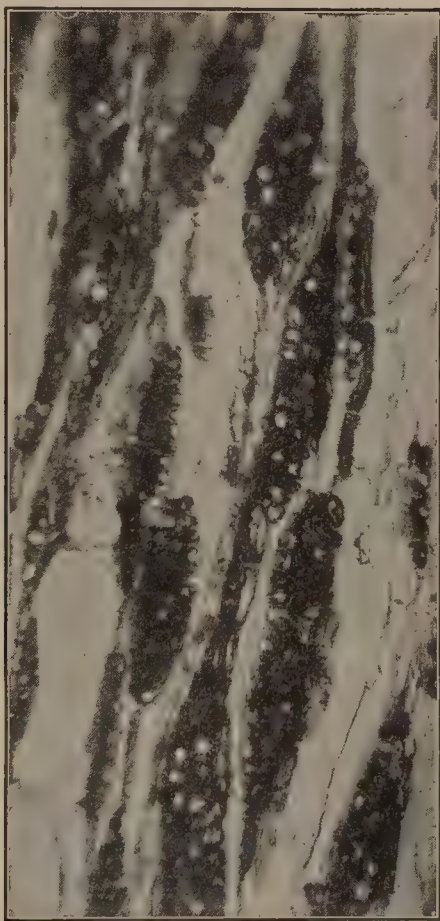


FIG. 213.—*N. discreta*, cross section of apple wood showing mycelium. After Cooper.

Xylaria Hill (p 207)

Stromata erect, corky or woody, simple or branched, black, with sterile stalk; perithecia in the upper parts of the stroma; asci 8-spored; spores 1-celled, black.

X. hypoxylon (L.) Grev.

A root rot of apple trees is due to a fungus closely related to the above named species, perhaps identical with it.

X. polymorpha and **X. digitata** are also reported in similar connection. Roots of affected trees are covered with a thin, white, compact, mycelial growth which soon develops into a black stroma. Black, anastomosing rhizomorphs radiate from the stroma several centimeters along the root; the cortex below is disintegrated and distal parts of the root die. The mycelium extends also into the wood, turning it brown.

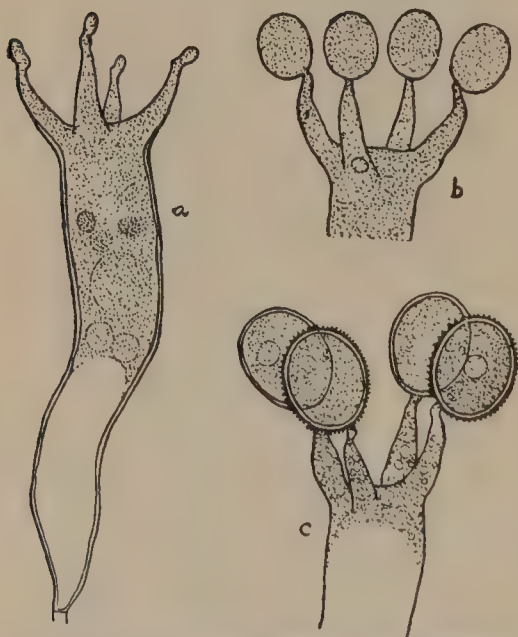
BASIDIOMYCETES (p. 56)

FIG. 214.—The typical basidium with sterigmata and spores in different stages of development. After de Bary.

The **basidium** is the distinguishing character of this class. It is typically a sporophore bearing short stalks on its distal end, the sterigmata, usually four, on which are borne spores, basidiospores, one on the tip of each sterigma, Fig. 214. In the great majority of genera the basidia are typical and are clearly recognizable as such.

In many of the lower basidiomycetes the basidia deviate somewhat from the typical form. Thus in the Hemibasidii, the smut fungi, the basidia are not typical in that they always arise from chlamydospores, not directly from the mycelium, Figs. 216, 226, and that they may produce more than the normal number of four sporidia and these

often from lateral, not terminal sterigmata. The basidia in the large group of rust fungi are also atypical.

The mycelium of the Basidiomycetes is septate and branched, and is always well developed. It is often found invading cells several meters from the sporogenous structures and frequently weaves together to form rhizomorphs.

Peculiar cell connections known as clamp connections, or knee joints, Fig. 218, are often found. The basidia in many genera are borne on large complex sporophores composed of the mycelial threads interwoven to form a false parenchyma. The spores may germinate by tubes or by budding.

Typical sexuality seems entirely wanting, even rudimentary or vestigial sexual organs, certainly recognizable, have not been found. The group is supposed in this regard, to represent the results of extreme simplification; the sexual organs to have long ago disappeared and the simple nuclear fusions that now exist to serve functionally as fertilization.

KEY TO THE SUBCLASSES OF **Basidiomycetes**

- | | |
|---|----------------------------------|
| Chlamydospores at maturity free in a sorus,
produced intercalary, from the mycelium;
basidiospores borne on a promycelium
and simulating conidia | 1. Hemibasidii , p. 211. |
| Chlamydospores absent or when present borne
on definite stalks
Basidia septate, arising from a resting spore
or borne directly on a hymenium | 2. Protobasidii , p. 230. |
| Basidia nonseptate, borne on a hymenium . . | 3. Eubasidii , p. 280. |

Hemibasidii

The Hemibasidii contain one order.

Ustilaginales ¹

Parasitic fungi, smut producers, mycelium consisting of hyaline, somewhat septate, branched, mostly intercellular filaments, practically limited to the interior of the host; at maturity often disappearing partially or wholly through gelatinization; fertile mycelium compacting into masses and giving rise to numerous chlamydospores formed from its contents. Sporidia rarely develop on the

¹ Clinton, G. P. North American Flora, 7: pt. 1 Ustilaginales. N. Y. Bot. Gard. 1906.

exterior of the host. Sori prominent, usually forming dusty or agglutinated spore-masses that break out in definite places on the host or more rarely remain permanently embedded in the tissues.

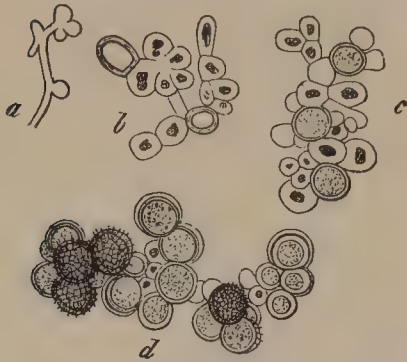


FIG. 215.—*Ustilago* spores showing development. After de Bary.

Spores (chlamydospores) light to dark colored, single, in pairs, or in spore-balls, the latter often composed in part of sterile cells.

The Ustilaginales are all parasites on higher flowering plants. The vegetative mycelium is mostly inconspicuous and is often distributed very widely in the host plant without giving external evidence of its presence until time of spore formation. It sends variously formed botryose or spherical haustoria into the host cells. At time of maturity of the fungus, the mycelium develops in great abundance at certain special places in the host, often in the ovary, leading to the development of large mycelial structures in the place of the host tissue.

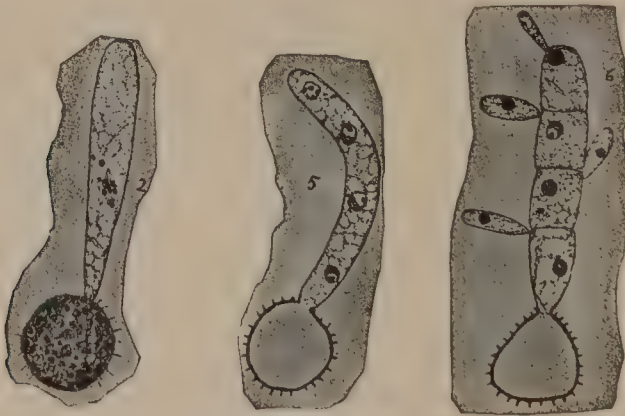


FIG. 216.—*Ustilago*. 2, promycelium with nucleus in mitosis; 5, with 4 nuclei; 6, with sporidia. After Harper.

The chlamydospores develop directly from the vegetative mycelium; new and numerous transverse cell-walls are formed; the resulting short cells swell, round off and become coated with a gelatinous envelope. This later disappears and the spores develop a new, thick, usually dark, double wall which is variously marked. The chlamydospores may be simple or compound, fertile or in

part sterile and are variously shaped and marked as described in the genera below.

The chlamydospores may germinate at once or after a more or less protracted rest interval. In germination in water or nutrient solution, manure water, etc., a short tube is protruded, the promycelium, this differing in character in the two families, Figs. 216, 226. From the promycelium of most species there develop **sporidia**, often called conidia, 1-12 or even more. The promycelium is regarded as homologous with the basidium of the other basidiomycetes and the sporidia as basidiospores.

The sporidia in suitable nutrient solutions often undergo repeated and indefinite budding closely simulating yeast cells in appearance. Fusion of sporidia is not uncommon. Fig. 217. Sporidia finding lodgment in suitable plant parts under suitable environmental conditions give rise to infection. The points at which infection can occur are very diverse with different species and will be considered under the separate species below.

The vegetative cells are binucleate in *Tilletia*, multinucleate in the *Ustilaginaceæ*. The young chlamydospores in the case of *Doassansia*, *Entyloma*, *Ustilago* and *Urocystis* are binucleate. These two nuclei, according to Dangeard, later fuse rendering the mature spore uninucleate. In germination the one nucleus passes into the promycelium, then divides mitotically, Fig. 216, 2. A second division gives four nuclei (Fig. 216, 5) the spore nuclei.

In the fusions of salsify smut sporidia, Federly has found an accompanying nuclear fusion, while Lutman finds similar fusion in the conjugating promycelial cells of oat smut.

Whether or not these nuclear fusions represent a sexual act is a much controverted point.

There are according to Clinton about four hundred species in America.

KEY TO FAMILIES OF *Ustilaginales*

Promycelium usually with sporidia lateral

at septa 1. *Ustilaginaceæ*, p. 214.

Promycelium with clustered terminal sporidia. 2. *Tilletiaceæ*, p. 222.



FIG. 217.—*Ustilago*. 17, sporidia fusing; 19, promycelial cells with fusion tube, apical cell disorganizing. After Harper.

Ustilaginaceæ (p. 213)

Sori usually forming exposed, dusty or agglutinated spore-masses; germination of chlamydospores by means of septate promycelia which give rise to terminal and lateral sporidia or else to infection-threads.

KEY TO GENERA OF Ustilaginaceæ

Spores single

Sori dusty at maturity

Without definite false membrane 1. **Ustilago**, p. 214.

With false membrane of definite fungous cells 2. **Sphacelotheca**, p. 220.

Ustilago (Persoon) Roussel

Sori on various parts of the hosts, at maturity forming dusty spore masses, usually dark colored; spores single, produced irregularly in the fertile mycelial threads which early entirely disappear through gelatinization, small to medium in size; germination by means of a septate promycelium producing only infection-threads or with sporidia formed terminally and laterally near the septa; sporidia in water usually germinate into infection-threads but in nutrient solutions multiply indefinitely, yeast-fashion.

About two hundred species, seventy-two of which are given by Clinton as occurring in America.

U. avenæ (Pers.) Jens.

Sori in spikelets, rarely in leaves, forming a dusty, olive-brown spore-mass, about 6–12 mm. long by half as wide, usually rather completely destroying floral parts, eventually becoming dissipated; spores lighter colored on one side, subspherical to spherical though often elongate, minutely echinulate, 5–9 μ in length. Widespread on oats.



FIG. 218.— *U. avenæ*, germinating in water. After Clinton.

The fungus was known by the name *Ustilago* as early as 1552 and was called *U. avenæ* in 1591. The species of *Ustilago* on oats, wheat and barley were considered identical until Jensen showed that they are not intercommunicable. Wolff

showed that seedlings can be infected through the first sheath leaf. Brefeld, studying infection more closely, found it to be accomplished by germ tubes from sporidia and that plants are free from

infection after the growing leaves have pushed one centimeter through the sheath leaf. The mycelium, after infection, grows through the plant until blooming time when it seeks the ovaries and the enclosing glumes in which it forms a mycelial mass, which soon changes into spores. In nutrient solutions the conidia bud indefinitely, while on the host plant they produce infecting hyphæ.

Germination occurs readily in water, a well developed promycelium resulting in about twenty-four hours, Fig. 218. The sporidia are mostly narrowly elliptical. Fusion of sporidia is common. The promycelia are usually four-celled and occasionally branch, especially near the base.

***U. crameri* Körn.**

Sori in the spikelets, infecting all of the spike, ovate, about 2-4 mm. in length, chiefly destroying inner and basal parts; spores reddish-brown, chiefly ovoid to subspherical though occasionally more elongate and irregular, smooth, with usually pitted contents, chiefly 8-11 μ in length. The

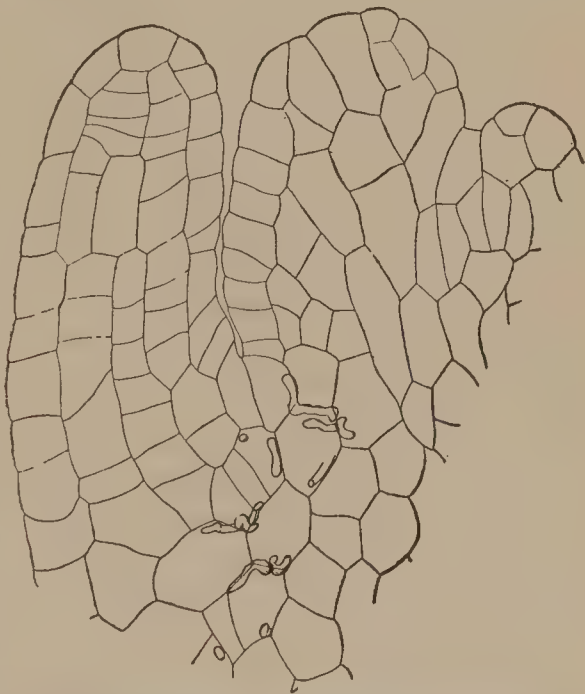


FIG. 219.—Growing point of the stem of barley, much enlarged, showing smut mycelium. After Hecke.

promycelium is much branched but no sporidia are produced.

The smut commonly affects the ovaries of *Panicum* and *Setaria*.

***U. crus-galli* T. & E.**

Sori often encircling stems at nodes or at the juncture of the inflorescence, infecting both stem and leaves, prominent, often nodular, one to several centimeters in length, protected by a tough, hispid membrane which upon rupture discloses an olive-brown, dusty spore-mass; spores ovoid to spherical, occasionally more elongate, rather bluntly echinulate or even verruculose, chiefly 10-14 μ in length.

On *Panicum crus-galli*.

U. sacchari Rab.

Spore-mass black, spores globose or angularly globose, 8–18 μ in diameter, olive-brown or rufous, epispore thick, smooth.

On sugar-cane throughout the tropics, especially in the old world.

U. hordei (Pers.) K. & S.

Sori in spikelets, forming an adhering purple-black spore-mass about 6–10 mm. in length, covered rather permanently by the transparent basal parts of the glumes; spores lighter colored on one side, usually subspherical or spherical, smooth, 5–9 μ , the most elongate rarely 9–11 μ in length. Common on barley.

This was first recognized as distinct from the oat smut in 1591 by Lobelius. In 1888 the species was separated from the other smut on barley.

The spores germinate freely in water by one, rarely two, tubes, usually 4-celled, and produce abundant sporidia; these increase by budding, produce germ tubes, or fuse with each other.

U. levis (K. & S.) Mag.

Sori in spikelets, forming a black-brown, adhering spore-mass sometimes small and entirely concealed by the glumes, but usually evident and destroying inner and basal parts; spores lighter colored on one side, subspherical to spherical or rarely elongate, smooth, 5–9 μ , the most elongate rarely 11 μ in length.

On oats, probably more common than records show as it is very difficult to distinguish from *U. avenae* from which it differs chiefly in its smooth granular spores.

U. macrospora Desm.

Sori in leaves and glumes, generally showing as linear striæ, but often more or less merged, at first covered by the epidermis, but this later rupturing and disclosing black-brown, dusty lines of spores; spores medium to dark reddish-brown, chiefly ovoid to spherical or occasionally somewhat irregular and elongate, coarsely verrucose, at circumference usually showing the projections as tinted, blunt, scale-like appendages, sometimes even semi-reticulate, 12–19 μ in length.

On various species of *Agropyron*.

U. nuda (Jens.) K. & S.

Sori in spikelets, forming a dusty, olive-brown spore-mass, about 6–10 mm. long by half as wide, temporarily protected by a thin membrane which soon becomes dissipated leaving the naked rachis

behind; spores lighter colored on one side, minutely echinulate, subspherical to spherical or occasionally elongate, 5–9 μ in length.

This smut on barley is distinguishable from the covered smut, *U. hordei*, by its olive-green spore-mass and by its early shedding of spores. As a rule each spikelet, except the awn and rachis, is entirely transformed into smut. In water and in nutrient solutions the spores germinate by a single promycelium, 1 to 3-septate, and often branched, but without sporidia. That infection is floral in loose smut of both wheat and barley was first shown by Maddox. The mycelium has been demonstrated in the embryo by Broili.

The spores falling between the glumes germinate, penetrate the ovary wall and into the growing point of the embryo. The mycelium here lies dormant until the seed germinates, when it grows keeping pace with the growing point throughout the season and finally invading the ovaries to produce its spores.

The infection of the pistil, the penetration of the integuments and the nucellus and embryo sac was followed in microtome sections by Lang. The embryo was reached by the mycelium some four weeks after infection of the pistil. In resting grains the mycelium is abundant in the scutellum as well as in all embryo parts except the roots.

Cross inoculation by Freeman and Johnson from barley to wheat and the reverse gave negative results. The optimum time for infection has been determined as the period of full bloom.

U. perennans Rost.

Sori in spikelets, more or less destroying the basal and inner parts, sometimes even running down on pedicels, oblong, about 3–8 mm. in length, with dusty, olive-brown spore masses; mycelium perennial in perennial parts of host; spores chiefly subspherical, occasionally ovate to ellipsoidal, usually lighter colored on one side, more or less minutely echinulate, especially on the lighter side, 5–8 μ in length.

On the tall oat grass.

U. tritici (Pers.) Rost.

Sori in spikelets, forming a dusty, olive-brown spore-mass, about 8–12 mm. long by half as wide, usually entirely destroying floral parts and eventually becoming dissipated and leaving behind only



FIG. 220.—*U. levis*, germination in modified Cohn's solution. After Clinton.

the naked rachis; spores lighter colored on one side, usually sub-spherical to spherical, occasionally elongate, minutely echinulate especially on the lighter side, 5-9 μ in length. On wheat wherever cultivated.

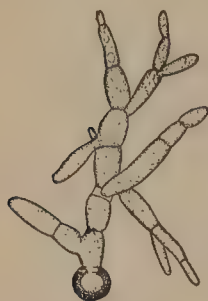


FIG. 221.—*U. tritici*, germination in modified Cohn's solution. After Kellerman and Swingle.

The smut mass is covered at first by a very delicate membrane. Infection is floral as described for *U. nuda*.

The spores germinate in water by a long, 2 to 3, or even 6 to 7-septate, promycelium, often curved. In nutrient solutions the promycelium branches profusely but sporidia are few or are entirely absent.

U. zeæ (Beck.) Ung.

Sori on any part of the corn plant, usually prominent, forming irregular swellings from a few millimeters to over a decimeter in diameter, at first protected by a sort of false, white membrane composed of host cells and semi-gelatinized fungous threads, soon rupturing and disclosing a reddish-brown spore-mass; spores ellipsoidal to spherical or rarely more irregular, prominently though rather bluntly echinulate, 8-11 μ , the most elongate 15 μ in length.

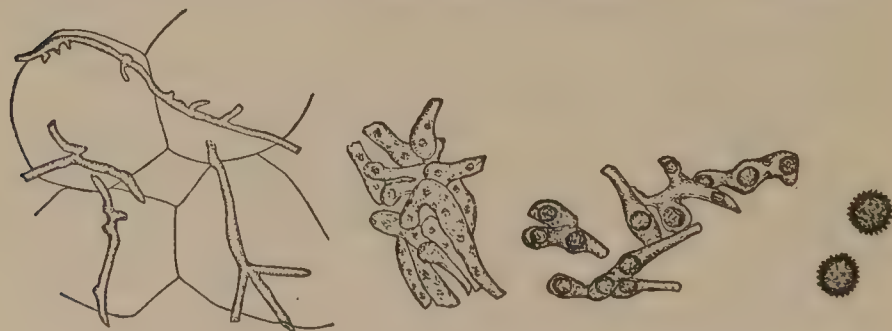


FIG. 222.—*U. zeæ*, stages in spore development. After Knowles.

The germination of the spores, which occurs but poorly in water, was first studied by Kühn in 1857 and in 1874 he saw the penetration of the germ tubes through the epidermis of the corn plant. Brefeld showed that the spores germinate well in nutrient solutions and that secondary spores are formed; also that corn can be infected by the sporidia at any point on its surface above ground when the tissues are soft and actively growing; and that infection is local on the host.

It is now known that the chlamydospores are capable of germination without hibernation and that they remain viable, one, two, perhaps more years. It was shown by Brefeld in 1895 that the chlamydospores produce conidia in the air freely. It is these, air-borne, arising from spores on the ground, manure, etc., which are chiefly responsible for infection. They must reach the plant on a susceptible part and under suitable conditions of moisture. The germ tubes from the sporidia penetrate the epidermis, grow through or between the cells, Fig. 222, with an irregular mycelium which branches profusely and calls forth great hypertrophy of the surrounding host tissue. In sporing, the mycelium forms a great number of short, slender, irregular branches which make up a close tangled network in the diseased tissue. These slender branches swell, gelatinize, and portions of them round off as spores, Fig. 222.

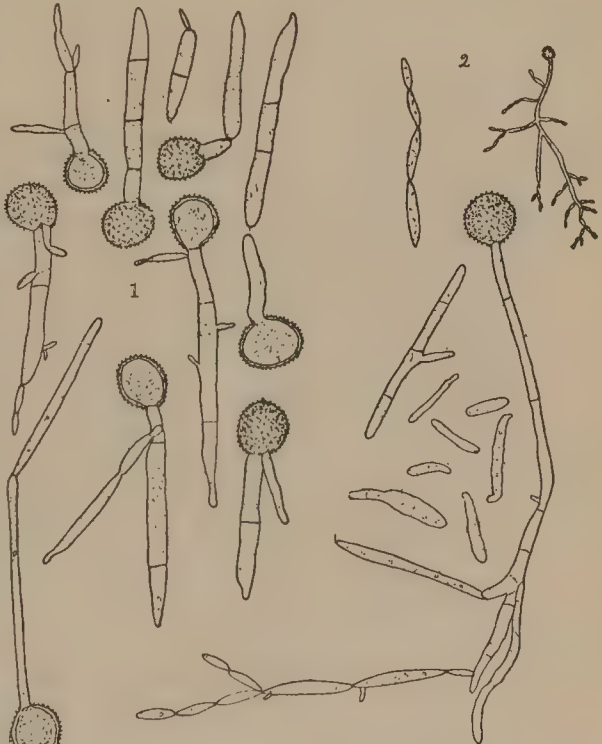


FIG. 223.—*U. zeæ*. 1, germination after three days in water; 2, similar but in air, showing air sporidia. After Clinton.

***U. striæformis* (West.) Niess.**

Sori in leaves, sheaths and rarely in the inflorescence, from short to linear, often extending, apparently by terminal fusion, for several centimeters, also occasionally fusing laterally to cover most of the leaf; at first covered by the epidermis but this is soon ruptured and dusty brown to black, linear masses of spores become scattered and the leaves become shredded; spores usually ellipsoidal to spherical, occasionally irregular, prominently echinulate, chiefly 9–14 μ in length.

It appears to be perennial. The spores germinate sparsely. The promycelium is long, branched, septate, and produces no sporidia. On red top, timothy and species of *Poa* and *Festuca*.

Other economic species of less import in America are in sorghum, barley, *Panicum*, bamboo, *Tragopogon*, tulip.

Sphacelotheca de Bary (p. 214)

Sori usually in the inflorescence, often limited to the ovaries, provided with a definite, more or less temporary, false membrane,

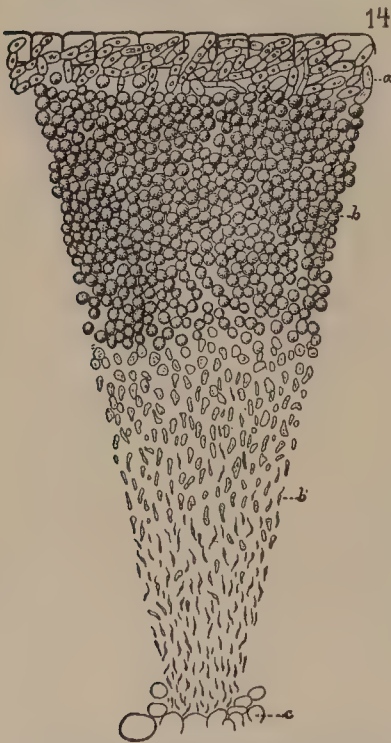


FIG. 224.—*S. sorghi*, cross section through base of young infected body (ovary). *a*, false membrane of epidermal cells and sterile mycelium, *b*, mature spores, *b'*, immature spores, *c*, columella. After Clinton.

covering a dusty spore-mass; and a central columella, usually formed chiefly of the host plant's tissues. The false membrane is composed largely or entirely of sterile fungous cells which are hyaline or slightly tinted, oblong to spherical and usually more or less firmly bound together; spores single, usually reddish-brown, developed in a somewhat centripetal manner as in *Cintractia*, small to medium in size; germination as in *Ustilago*.

Sixteen species are recorded by Clinton for America. Of these only three are of economic importance. By Lindau the genus is not separated from *Ustilago*.

Sphacelotheca sorghi (Lk.) Cl.

Sori usually in the ovaries or stamens forming oblong to ovate bodies 3–12 mm. in length, rarely fusing the very young spikelets into irregular forms, protected for some time by a false membrane

upon the rupture of which the olive-brown spore-mass becomes scattered, leaving naked the distinct columella of plant tissue. The sterile cells of the membrane break up to some extent into groups, hyaline, oblong to subspherical, chiefly 7–18 μ in length;

spores subspherical to spherical, smooth, contents often granular, $5.5\text{--}8.5\ \mu$ in diameter.

On Johnson grass and sorghum throughout the world.

The young pistil and usually the stamens as well are displaced by the fungous mycelium, the two being often blended together. The spores germinate readily in water, either when fresh or a year old, showing papillæ in from three to ten hours. The promycelium is 2 to 3-septate and from the ends of one or more of its cells narrow tubes appear. These later fuse with the adjacent cell, forming the "buckle joints." Either infection tubes or sporidia may also



FIG. 225.—*S. reiliana*, longitudinal section of a growing point showing position of hyphæ. After Gilbert and Potter.

arise from the promycelium. Infection is possible only with young plants.

The mycelium in the host plant grows rapidly into long irregular, hyaline, thin-walled threads 2–4 mm. thick, which run through and between the cells. It is most abundant in the parenchyma, advancing especially through the pith region with the growth of the host. The young ovaries and stamens are eventually reached and the mycelium there develops richly under the epidermis. The outer cells remain sterile and constitute the membrane; the inner gelatinize and develop into spores.

S. reiliana (Kühn) Cl.¹

Sori very prominent forming irregular masses including more or less of the entire panicle, usually 5–15 cm. in length; often at first protected by the leaf-sheath. A whitish, false membrane encloses the black-brown spore-mass and the ray-like remains of the peduncles or columellas. In time it becomes ruptured and the spores scattered. Sterile cells are also scattered in groups through the spore-mass, chiefly subspherical, 7–15 μ in diameter; spores somewhat opaque, chiefly subspherical to spherical or occasionally ovoid or slightly angled, minutely but abundantly verruculose, 9–14 μ in length.

This is a cosmopolitan but comparatively rare form on corn, affecting the ovaries. It occurs also on sorghum. In germination a 3 to 4-celled, often branched, promycelium is formed and sporidia are produced.

The host is infected while young, but not from seed borne spores, and the disease is systemic, the lateral buds carrying the infection in their meristematic tissue.

S. diplospora (E. & E.) Cl. is found on *Panicum crus-galli* and related grasses in the lower Mississippi Valley.

Tilletiaceæ (p. 213)

Sori either forming dusty, erumpent spore-masses or permanently embedded in the tissues. Germination by means of a short promycelium which usually gives rise to a terminal cluster of elongate sporidia, that, with or without fusing in pairs, produce similar or dissimilar secondary sporidia or germinate directly into infection threads.

The American Tilletiaceæ embrace nine genera and about one hundred twenty-five species.

KEY TO GENERA OF Tilletiaceæ**Spores single**

Sori dusty at maturity; spores without a conspicuous hyaline appendage 1. *Tilletia*, p. 223.

Sori permanently embedded in the tissues, definite, small 2. *Entyloma*, p. 229.

Spores in balls

Sori dusty; spore-balls with sterile cortex . . . 3 *Urocystis*, p. 225.

Sori rather permanently embedded in tissues, spore-balls with sterile cortex 4. *Doassansia*, p. 230.

¹ Potter, A. A. Head smut of sorghum and maize. Jour. Agr. Res. 2: 339, 1914.

Tilletia Tulasne (p. 222)

Sori in various parts of the host, usually in the ovary, forming dusty spore-masses; spores single and usually formed singly in the ends of the mycelial threads which disappear more or less completely through gelatinization, germination usually by a short promycelium which bears a terminal cluster of elongate sporidia that in nutrient solutions, with or without fusing in pairs, may give rise to a considerable mycelium bearing secondary air-sporidia.

The genus closely resembles *Ustilago* except in its larger spores and mode of germination.

Twenty-two American species are listed by Clinton. Only four are of economic importance.

***T. lævis* Kühn**

Sori in ovaries, ovate or oblong, 5-8 mm. in length, more or less concealed by the glumes, all or only part of the ovaries of a spike infected; spores light to dark-brown, oblong to chiefly subspherical or spherical, occasionally somewhat angular, foetid, especially when young, smooth, chiefly 16-22 μ , the most elongate rarely 28 μ in length.

On wheat wherever grown.

Infection occurs as in oats in the very young plants. From the infection point the mycelium approaches the growing point and follows the development of its host, sending its branches into each spikelet and finally into the growing ovules. Here it develops a close knot and in the ends of the threads and in the short branches the spores form. The spores germinate by a rather long, continuous, thick promycelium on the tip of which a crown of long slender sporidia develops. The sporidia soon become arched and often fuse in pairs; they develop infection threads.

***T. tritici* (Bjerk.) Wint.**

Sori in ovaries, ovate to oblong, 5-8 mm. in length, more or less concealed by the glumes; sterile cells few, hyaline, sub-spherical,



FIG. 226.—*T. lævis*. A, germinating spore producing sporidia; B, Sporidia which have united. One has produced a secondary sporidium at x and this is sending out an infection thread. After Freeman and Stedman.

with medium-thin wall, smaller than the fertile cells, which are chiefly subspherical, light to dark-brown, with winged reticulations about $1\ \mu$ high by $2\text{--}4\ \mu$ wide, and are $16\text{--}22\ \mu$ in diameter.

Common on wheat, occasional on rye.

Experiments have shown this to be distinct from *T. l  vis* which it closely resembles except for its reticulate spores.

***T. texana* Long**

Sori in ovaries, ovoid or oblong, about 3–5 mm. in length, more or less hidden by enveloping glumes, forming a somewhat agglu-



FIG. 227.—*Tilletia tritici*. A, Two spores germinated in moist air, promycelium and sporidia, several of which have fused in pairs. Secondary sporidia at C. B, Spores germinated in water, promycelia elongate, septate. The protoplasm passes over into the younger cell. After Tubeuf.

minated, light-reddish-brown spore-mass; sterile cells not very numerous, hyaline, with very thick, often lamellate walls; fertile cells very light colored, orange-yellow appearing as if immature, chiefly subspherical or spherical, with prominent conical tubercles which extend out $2\text{--}3\ \mu$, chiefly $19\text{--}25\ \mu$ in diameter, including envelope.

On *Hordeum nodosum* in Texas.

***T. horrida* Tak.**

Sori in the ovaries more or less destroying them, completely concealed by enveloping glumes; spores usually present in different stages of development, the mature spores almost opaque, chiefly subspherical to spherical, with very coarse hyaline or slightly tinted, somewhat curved scales which show at the circumference

of the spore as a band about $2-4\ \mu$ wide and on its top as polygonal areas $2-3\ \mu$ across; hyaline membrane more or less evident and often at one side in a short thread-like projection, $22-33\ \mu$ in length.

Cross sections of stems bearing smutted heads reveal the mycelium in the chlorophyll parenchyma between the fibrous tissue.

On rice.

Urocystis Rabenhorst (p. 222)

Sori usually in the leaves or stems, occasionally in other parts, producing dark-colored, usually dusty, spore-masses; spore-balls permanent, composed of an enveloping cortex of tinted sterile cells and usually one to several interior fertile cells; fertile cells generally dark-colored; germination often by a short promycelium which produces terminally-grouped sporidia; these give rise to similar secondary sporidia or to infection-threads.

U. cepulæ Frost.¹

Sori in leaves, forming isolated pustules or affecting them for the greater part of their length and breadth, sometimes occurring

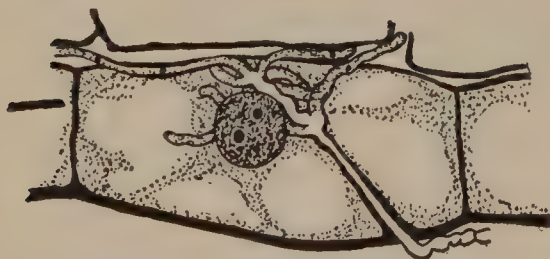


FIG. 229.—*U. cepulæ*. Showing infection through the epidermal cell, from the outside of the cotyledon, the hypha seeking the nucleus. After Anderson.



FIG. 228.—Spore balls of *U. cepulæ*. After Thaxter.

at their bases, in the bulbs. Upon rupture of the covering membrane a dusty, black-brown spore-mass appears; spore-balls ovoid to spherical, $17-25\ \mu$ in length; sterile cells tinted, ovoid to spherical, small, rather completely covering the spores, usually

$4-8\ \mu$ in length; fertile cells reddish-brown, ovoid to spherical, usually 1, rarely 2 in a ball, chiefly $12-16\ \mu$ in length. On *Allium*.

Infection usually occurs within 2 weeks after planting, and seedlings are not susceptible after the 17th day. It probably is always through the cotyledon.

The fungus once through the epidermis remains intercellular, spreading in all directions, sending occasional haustoria into the host cells.

¹ Anderson, J. P. Development and pathogenesis of the onion smut fungus. Mass. Agr. Exp. Sta. Tech. Bul. 4, 1921.



FIG. 230.—*U. cepulæ*. Stages of sporogenesis. A–P, development of a hooked cell and origin of the enveloping hyphæ. Q, section through a young spore; R, surface view of a young spore; S, section through a mature spore. After Anderson.



FIG. 231.—*U. cepulæ*, germination of spores. After Anderson.

As the time for spore formation approaches the mycelium masses between the cells and branches profusely, forming twisted tangles which develop into the spore masses, the mycelial cells changing directly into spore cells by the intricate steps shown in Fig. 230.

In germination the central spore produces a hemispherical vesicle (Fig. 231), the promycelium, from which branches arise. Sporidia if they occur are rare.



FIG. 232.—Germination of spores of *Urocystis tritici*. After Noble.

The fungus can live saprophytically in soil probably for years.

***U. tritici* Koern.¹**

Sori in leaves, leaf-sheaths, stems and occasionally on glumes, forming elongated parallel streaks, at first covered by the raised, leaden-colored epidermis, which gradually decays in patches allowing the escape of the black, powdery spores. Spore-balls

¹ Noble, R. J. Studies on the parasitism of *Urocystis tritici* Koern., the organism causing flag smut of wheat. Jour. Agr. Res. **27**: 451, 1924.

globose, ellipsoid or oblong, bright golden brown, variable in size and shape, $16-40\ \mu$ diam., or $24-40 \times 24-32\ \mu$ averaging $32 \times 24\ \mu$; spores spherical or oval, 1-4 in a ball, occasionally 5, $9-12\ \mu$ in diameter, or $12-16\ \mu$ long; sterile peripheral cells generally completely investing spores, pale yellow, ellipsoid to globose, and bulging, $9-12\ \mu$ long.

On wheat causing flag smut.

This species is mainly separated from *U. occulta* biologically. The spores are commonly two in a ball, although three and four are also found. The investing layer of sterile cells is generally complete. The spore is delicately punctulate on the surface, but this is more marked in *U. occulta*.

U. occulta (Wallr.) Rab.

Sori in leaves, especially in the sheaths, culms and inflorescence, forming linear striæ usually of great length and often merged into a continuous stratum of dusty, reddish-black, spore-balls; spore-balls oblong to subspherical, $16-32\ \mu$ in length; sterile cells often incompletely covering the spores, hyaline or yellowish, subspherical to oblong, usually with distended and uniformly thickened walls; fertile cells reddish-brown, oblong to subspherical, often flattened, smooth, 1 to 4 in a ball, $11-18\ \mu$ in length.

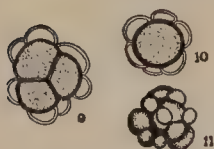


FIG. 233.—Spore balls of *U. occulta*. After Thaxter.

On rye wherever cultivated, though not common in America.

The seat of spore formation is most often on the stems or sheaths, though all aerial parts of the plant are susceptible. In the vegetative parts the fungus is commonly found in the tissue between the vascular bundles.

U. violæ (Sow.) F. de W.

Sori on stems, rootstocks, petioles and leaves of violets forming prominent irregular swellings.

U. agropyri (Preu.) Schr.

Sori in various parts, commonly in leaves, forming striæ, which may be distinct or cover the surface of the leaf; at first lead-colored and protected by the epidermis but soon rupturing and scattering the reddish-brown spores; spore-balls oblong to subspherical, $16-32\ \mu$ in length; sterile cells hyaline to yellowish, oblong to subspherical, usually completely covering the fertile cells, outer wall thin and by collapsing giving a ridged effect to the covering; spores 1 or 2, rarely 3 or 4 in a ball, reddish-brown, oblong to subspherical, often flattened, smooth, $11-18\ \mu$ in length.

On Agropyron and some other coarse grasses.

Other species are on Gladiolus, Ornithogalum, pansy, primrose.

Entyloma de Bary (p. 222)

Sori usually foliar, generally forming discolored, but not distorted areas, permanently embedded in the tissues; spores single, produced terminally or intercalary in the mycelium which does not entirely disappear through gelatinization, free, sometimes irregularly adhering through pressure, hyaline to yellowish or reddish-yellow, rarely dark-colored, germination by a short promycelium bearing a terminal group of sporidia which usually conjugate in pairs and produce secondary sporidia or infection-threads; sporidia often formed by germination of the spores *in situ*, the promycelium protruding through the stomata.

Twenty American species are recorded.

E. crastophilum Sacc.

Sori in leaves, subcircular to linear, about 0.25–2 mm. in length, usually distinct though occasionally merged, black, long covered by the epidermis; spores dark-brown, tightly packed and adhering more or less, chiefly ovoid to spherical or angled through pressure, rather thick-walled, 8–14 μ in length.

On Poa, Phleum, Agrostis and other grasses.

E. irregulare Joh. also occurs on species of Poa; **E. polysporum** (Pk.) Farl. on sunflower.

E. ellisii Hals.

Sori in leaves, forming pale white spots, indefinitely limited,



FIG. 234.—*E. ellisii*, chlamydospores germinating within the leaf tissue, sporidia superficial. After Halsted.

subconfluent; spores hyaline or slightly yellowish, clustered in the intercellular spaces beneath the stomata, spherical, thick-walled, (2–5 μ) chiefly 16–20 μ but varying from 11–25 μ in diameter;

sporidia hypophyllous, abundant, acicular, small, 10-14 μ by less than 1 μ .

On spinach.

The chlamydospores germinate *in situ* beneath the stomata and bear the sporidia on tufts of promycelia which emerge through the stomata, presenting much the appearance of a Hyphomycete.

Other species are on beet, *Poa*, *Physalis*, *Solanum*, poppy, and various water-lilies.

Doassansia Cornu (p. 222)

Sori in various parts of the host, usually in the leaves, rather permanently embedded in the tissues; spore-balls conspicuous, permanent, consisting of a distinct cortical layer and a central mass of fertile cells entirely filling the interior, or with the innermost cells supplanted by parenchymatous cells or hyphal threads; spores hyaline or yellowish, with smooth, usually thin, walls; germination often *in situ*, by means of a short promycelium which gives rise to a terminal group of elongate sporidia, these often bearing secondary and even tertiary groups.

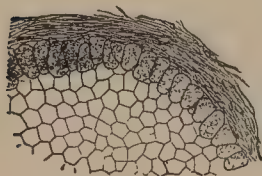


FIG. 235.—*Doassansia*. Part section through a spore ball showing sterile and fertile cells. After Dietel.

D. gossypii Lagerh. is on cotton.

Graphiola Poit. on various palms, is usually referred, doubtfully, to the Ustilaginales.

Protobasidii (p. 211)

Uredinales ^{1, 2, 3, 4}

The order is separated from the other orders of the Protobasidii by the basidia which arise from chlamydospores and have transverse septa. It is further characterized as follows.

Small fungi, mostly microscopic, parasitic in the tissues of ferns and seed plants. Mycelium much branched, septate, and with haustoria. Spores mainly borne in sori below the surface of the host, or rarely single within the host. Sori naked or covered

¹ Klebahn, H. *Die Wirtwechselnden Rostpilze*, Berlin, 1904.

² Sydow. *Monographia Uredinearum*, Leipzig, 1904.

³ Arthur, J. C. *North American Flora, Uredinales*, 1907.

⁴ Grove, W. B. *The British Rust Fungi*. Cambridge University Press, 1913.

at times, enclosed by peridia or paraphyses. Spores of five morphological sorts, not all present in every genus; (1) basidiospores, minute, thin-walled, without surface sculpturing, (2) pycniospores, small, smooth, of unknown function, (3) æciospores, verrucosely sculptured, borne in chains, (4) urediniospores, echinulately or verrucosely sculptured, borne singly, or sometimes in chains, (5) teliospores, smooth or variously sculptured, borne singly or in chains.

The order of some two thousand species, constituting the "rust" fungi, many of them living on cultivated plants of high value, is of great economic significance. Its members are strict, obligate parasites which in no stage of the life except in the promycelial stage can develop other than on the living host. The complexities of the life histories of the species, with their five distinct spore forms, inhabiting at different seasonal periods two different host plants, renders the order both difficult and exceedingly interesting.

The life history of the most complete of these fungi may be stated as follows:

I. *Æcia* (*æcidia*) and *O. pycnia*, often called spermogonia or pycnidia. The mycelium arising from a basidio-

spore invades the host plant and vegetates until vigor sufficient to spore formation is attained, meantime often producing local spotting, hypertrophy, or other injury to the host. The mycelium then develops a stroma which produces spore beds, **sori**, and ruptures the epidermis. These sori are usually deeply sunken in the host and cup-shaped and take the common name "cluster cups," Fig. 236, technically *æcia*, or *æcidia*. The sporophores arise from a hyphal plexus at the base of the cup and the spores are borne catenulate in acropetal succession. The whole structure is usually red or yellow. The outer layer of the cup usually consists of a

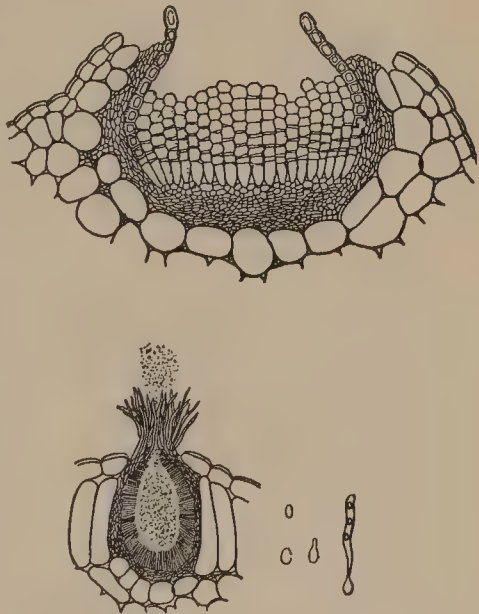


FIG. 236.—Æcium and pycnium. After Tavel.

palisade of sterile sporophores bearing sterile cells and constitutes the **peridium**. The **æciospores** are usually nearly globular, or angular by compression, reddish and rough and sometimes bear germ pores. They are capable of germination at once and on germination give rise to germ tubes which may infect susceptible hosts, leading to a mycelium. This in turn again produces sori which in some species may be *æcia*, in others *telia*, but in most species, *uredinia*.

Associated with the *æcia*, occasionally with other spore forms, but never borne alone, are minute **pycnia** with sporophores arising from their walls and bases. These bear unicellular pycniospores. Sterile hairs usually protrude from the ostioles. The whole structure in gross appearance is much like the pycnidium of *Phoma* or *Phyllosticta* but it is reddish or orange in color. These pycnia were formerly spoken of as "spermogonia" and the spores as "spermatia," due to the thought that they stood for degenerated male organs. Germination has now been observed and fertilization is known to occur elsewhere in the life-history and there is no longer reason to regard them as sexual organs.

II. **Uredinia (uredo-sori)**. The *æciospores* may infect the same species of plant that produced the *æciospores* (**autoëcious**) or plants of an entirely different species (**heteroëcious**). The mycelium produced by the *æciospore* develops within the host, usually remains local, and causes spotting. When it has attained sufficient vigor and age, usually after about two weeks, it produces a subepidermal hyphal plexus from which arises a bed of sporophores which bear unicellular, hyaline to brown, globose or elongated, usually sculptured spores, each with from 2 to 15 germ-pores variously placed. These are the urediniospores borne in **uredinia (uredo-sori)**. They may germinate at once producing a germ tube which develops to a mycelium.

These spores falling on susceptible tissues, by infection, usually stomatal, continue the production of *uredinia* and spread the disease. The urediniospores are usually short-lived and function to spread summer infection. They continue to form throughout the growing season.

In a few species there are what are known as **amphispores** or resting forms of urediniospores provided with thickened walls. They have colorless contents and pedicels more persistent than those of the usual urediniospore.

III. **Telia (teleuto-sori)**. Toward the latter part of the growing

season another kind of spore appears, often in the same sorus with the urediniospore and from the same mycelium. It is of various forms in different genera, one or more-celled, varies in shape, thickness of wall, surface marking, color, etc., but is uniform in the character of the germination which is very different from that of any of the other rust-spores.

In **teliospore** germination, typically each cell of the teliospore sends forth one germ tube. These tubes soon cease growth and by septation become 4-celled. Each cell then sends out a short branch, sterigma, on which there develops one round or oval, 1-celled, thin-walled spore, the **basidiospore**, often in this group called the **sporidium**.

Morphologically the promycelium is a basidium bearing its four sterigmata and four basidiospores. Relationship is thus shown on the one hand to the Ustilaginales, on the other hand to the Auriculariales, an assumption that is borne out by cytological evidence. Deviations from the typical mode of germination are found in several genera mentioned below (e. g., *Coleosporium*).

Basidiospores germinate immediately by germ tubes which on suitable hosts give rise again to pycnia and æcia or in some species to other spore forms completing the life cycle.

The most complex life cycle is thus seen to comprise pycniospores, æciospores, urediniospores, teliospores and basidiospores. For brevity the first four stages are commonly designated by the following symbols:

- O. Pycnia or pycnial stage
- I. Æcia or æcial stage
- II. Uredinia or uredinial stage
- III. Telia or telial stage

The spores in all cases, except those of the basidiospores and pycniospores arise directly from the mycelium.

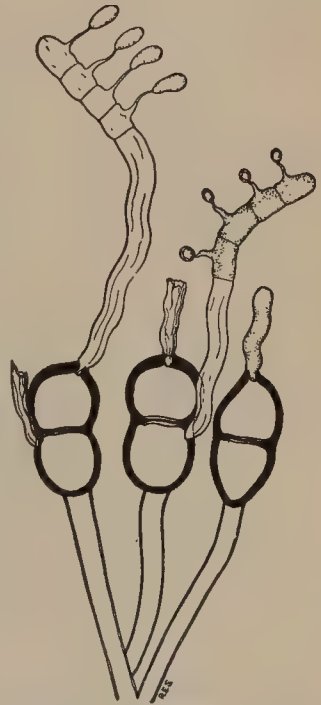


FIG. 237.—Germination of teliospores of *P. asparagi*. After Smith.

Mesospore is a term applied to occasional unicellular forms of teliospores found in *Puccinia* and related genera which do not usually have unicellular teliospores.

As has been said the pycniospores seem to be functionless though by some it is thought that they do function but that man has yet failed to find the conditions under which they readily germinate and cause infection. The æcial stage appearing first,

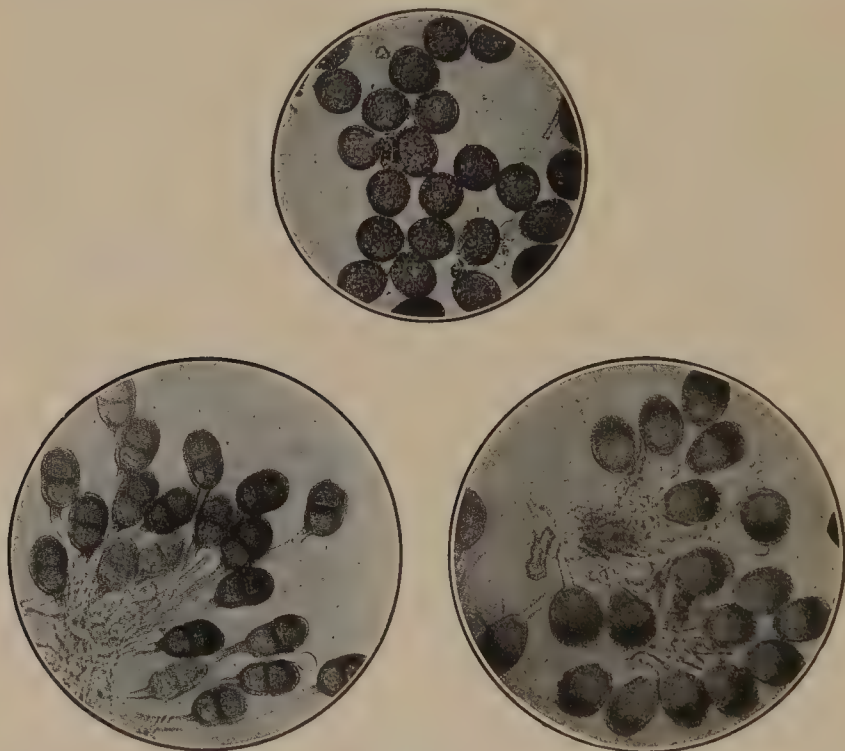


FIG. 238.—Amphisporcs, urediniosporcs and teliosporcs of *Puccinia vexans*.
After Holway.

and thus commonly in the spring, is often called the “spring stage.” It serves as an early stage to propagate and spread the fungus. The uredinia, often called the “summer stage,” constitute the phase usually of longest duration and of most injury. Its function is preëminently to multiply and spread the fungus.

The telia, often called the “winter stage,” usually, but not always, constitute the resting, hibernating stage. In many instances the teliospores must rest over winter before they are capable of germination. Classification is based primarily on the teliospores.

While all five of the spore forms discussed above are typical of many species there are many other species which do not possess all of these forms or indeed which may possess only one spore form.

Schröter for convenience groups the rusts, according to the spore forms that they show, under the following type names though it must be recognized that such grouping is purely artificial and does not necessarily bring together closely related species.

Eu-type	O, I, II, III present;	
Brachy-type	O, II, III present;	I omitted.
Opsis-type	O, I, III present;	II omitted.
Hemi-type	II, III present;	O, I omitted.
Micro-type	only III present;	germination only after a resting period.
Lepto-type	only III present;	germination without a resting period.

As examples of the above we have the following:

Eu-type, *Puccinia asparagi*, O, I, II, and III, all on Asparagus.

Brachy-type, *Puccinia suaveolens*, O, II, and III, all on thistle.

Opsis-type, *Puccinia podophylli*, O, I, and III, all on May apple.

Hemi-type, *Puccinia antirrhini*, II, and III, both on snapdragon.

Micro-type, *Puccinia ribis*, III, on Ribes.

Lepto-type, *Puccinia malvacearum*, III, on hollyhock.

Hundreds of the hemi-types will doubtless be revealed by study to be heteroecious eu-types, while the micro and lepto-types each represent conglomerates of two different groups; one group of short-cycled rusts, possessing pycnia and telia, and another group in which telia only are known.

Heteroecism.¹ All of the examples just given are **autoecious**, i. e., all known spore forms are found on the same species of host plant. In many other rusts, however, **heteroecism** prevails, i. e., one stage of the fungus is found on one species of host and another stage upon another host; rarely three host plants are involved in the cycle. Aside from the rusts only one other fungus (*Sclerotinia ledi*) is known to show heteroecism.

¹ Arthur, J. C. Cultures of Uredineæ. 1899-1917. *Mycol.* **13**: 232, 1921.

Heterœcism has been experimentally proved in some two hundred cases and may be assumed to exist in many cases not yet investigated.

Examples of heterœcism are as follows:

	Stages O, I.	Stages II, III.
Eu-type, <i>Puccinia graminis</i> ,	Berberis	Wheat
" <i>triticea</i> ,	Thalictrum	"
" <i>sorghii</i> ,	Oxalis	Corn
<i>Uromyces pisi</i> ,	Euphorbia	Pea
Opsis-type, <i>Gymnosporangium</i>		
<i>Juniperi-virginianæ</i>	Apple	Red cedar (III)

It frequently happens that part of the life cycle is passed upon a monocotyledonous plant, the remainder upon a dicotyledon.

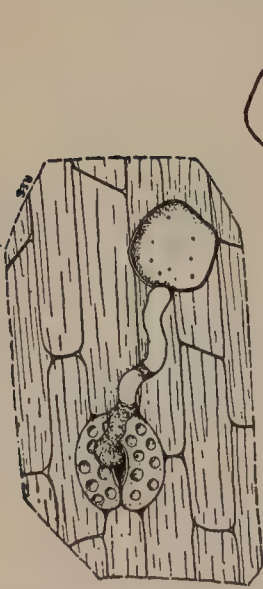


FIG. 239.—Urediniospore of *P. asparagi* germinating on surface of plant, and separate spores. After Smith.

In such event it is more often the II and III stages that are on the monocotyledon while the O and I stages are on the dicotyledon; examples of this are afforded in the numerous rusts of grasses, sedges and rushes. In one group the pycnia and the æcia are on pines (*Peridermium*), while the other stages are on dicotyledons. In the *Gymnosporangium*s the pycnial

and æcial stages are on Rosaceæ; the telial on *Juniperus* and its kin. While a few general rules can be worked out concerning host relations there are many exceptions and to know one stage of a heterœcious rust generally gives little or no clue to what its complementary host may be.

The mycelium of the rusts is usually intercellular and local though in a few instances it is extensive and even perennial in

the host. It is abundantly branched, closely septate, gives off haustoria and usually bears numerous oil drops to which the dissolved carotin imparts a yellow or orange color.

Irritation by the mycelium often induces marked hypertrophy or even witches' brooms or other deformation of the host. Hypertrophy is most common with the æcia but may result from the telia as well, as is conspicuously shown in the genus *Gymnosporangium*. In some instances the whole habit of the host plant is altered by the presence of the mycelium so as to render it almost unrecognizable, e. g., the æcium of *Uromyces pisi* on *Euphorbia*.

The host cells are seldom killed by the mycelium, which abstracts its food supply from the carbohydrates and other nutrients of the cell sap without direct injury to the protoplasm, though ultimately there is serious effect upon both growth of the host and its seed production.

Cytology. The mycelial cells of the rusts are binucleate, a condition which begins just below the æcium. The origin and significance of this condition is of much interest.

In all of the rusts so far investigated that have an æcium or primary uredinium there is in the æcio-mycelium or the primary uredinio-mycelium a fusion of uninucleated cells, gametes. This cellular fusion is not, however, followed by a nuclear fusion until after long delay; but the two nuclei remain in the fusion cell and when this cell divides both nuclei divide mitotically and simultaneously but still independently of each other, **conjugate division**. This process continues through the æcial sporophores, or uredinial sporophores, and in the production of the spores, with the result that the cells of all of these are binucleate. The conjugate division continues further through the uredinia and until teliospore formation occurs, the

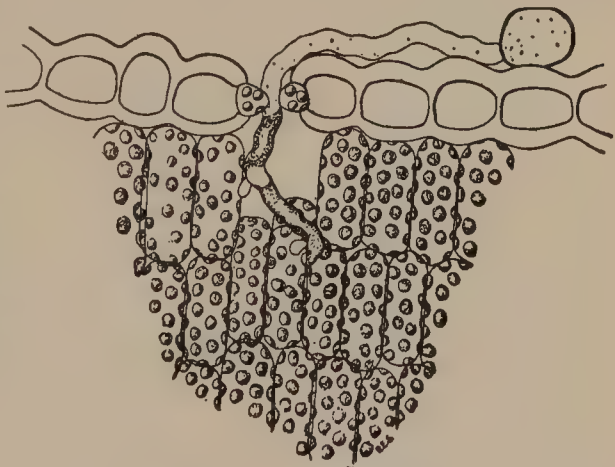


FIG. 240.—Cross section, showing infection from spore of *P. asparagi*. After Smith.

whole intervening series of cells being binucleate. Prior to the formation of the promycelium and in the teliospore the nuclei unite, reducing the cells again to an uninucleate condition.

In rusts which have only teliospores the binucleate condition begins somewhere in the mycelium from which the teliospores arise.

It is generally held that the cellular fusion is a sexual act with long delayed fusion of the sexual nuclei, and consequently that the uninucleate phase is the gametophyte; that the beginning of the binucleate condition marks the origin of the sporophyte.

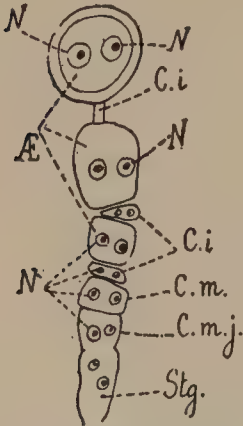


FIG. 241.—Showing conjugate nuclei and degenerating cells in conidiospore chain of *Aecidium*. After Sappin-Trouffy.



FIG. 242.—*Gymnosporangium clavariæforme*, mitosis of a nucleus in the promycelium. After Blackman.



FIG. 243.—Conjugate nuclear division in *Gymnosporangium clavariæforme* showing four chromatin masses. After Blackman.

A word may here be given to the usually discredited **mycoplasma theory** of Eriksson. This affirms the existence in the cells of wheat grain of an intimate mixture of rust protoplasm and host protoplasm. This mycoplasma may rest thus for months. Finally the host-cell nucleus becomes digested and the fungous plasm develops to a mycelium which proceeds to invade the surrounding tissues of the seedling as these develop on germination of the seed.

Biologic specialization much as is found in the Erysiphales occurs also in the Uredinales. There are many species, each of which is found on a large number of hosts. Upon its numerous hosts the fungus may show no morphological variation, yet attempts to inoculate from one host to another may uniformly give negative results.

It further often occurs that one stage, e. g., the æcia of a species may grow upon only one host while the uredinia or telia may grow upon many different species of hosts; and in such cases that æciospores which have arisen on host X, from infection with spores from host A, are capable of infecting host A and that host only; while æciospores which have arisen on host X, by infection with spores from host B, are capable of infecting host B and only this host; and so on for numerous forms.

An excellent example of such biologic specialization is offered in the common pine Peridermium. Æcia may be produced upon the pine by sowing of *Coleosporium* teliospores from *Senecio*, *Campanula*, *Pulsatilla*, etc., but the æciospores which develop on the pine are capable of infecting only those species of hosts from which the teliospores were taken.

Similarly Eriksson has determined that though rusts from many grains can infect the barberry, the æciospores there produced are not capable of infecting plants of species other than those from which the fungus was derived, or at most they can



FIG. 244.—Conjugate nuclear division in cells of *Puccinia podophylli*. After Christman.

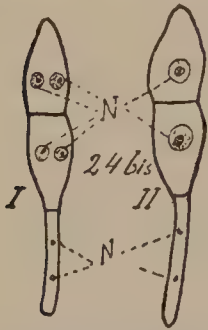


FIG. 245.—Diagrammatic representation of fusion of nuclei in the teliospore. After Delacroix and Maublanc.

infect but a very limited number of species. Further proof of the existence of biologic forms has recently been presented by Stakman.

Infection Experiments. Since the method of studying the rusts by observing their life histories in the laboratory where they are under complete control of the observer has assumed such prominence of late years the technique deserves notice. The first step is to find associated in the field the æcia and other stages of a rust in such way as to suggest relationship between two forms hitherto unknown to be connected.

Material of the rust is then collected and healthy host plants are also removed to the laboratory. If the teliospores are col-

lected in the fall they are kept out of doors in cheese cloth bags till germination time in the spring. Whether collected in spring or fall the viability of the spores must be tested by showing in a hanging drop of water. If germination is plentiful then the infection experiment is made. First the suspected alternate host is sprayed with water to give the spores proper conditions for germination, then masses of spores are placed directly on the plant by a scalpel and a bell jar is placed over the plant to assure a humid atmosphere. In from five to eight days yellow spots should



FIG. 246.—Urediniospores in *Rubus* showing nuclear conditions. After Blackman.

indicate where the infection has taken place and in a short time pycnia and æcia or other sori follow. In all infection work it is imperative to know that the plants used are not already infected in the field from another source.

Form Genera. The telial stage is the one on which classification is often based. Thus an æcium, uredinium, cœoma, etc., that is known to possess a telial form is regarded as part of the species indicated by its teliospore, e. g., *Æcidium berberidis* being part of *Puccinia graminis* has no specific identity but is regarded as a stage of *P. graminis*.

There are numerous uredinia, æcia and other non-telial forms of which the telial stage is not yet known. It becomes necessary for the present, for convenience of reference, to have names by

which to designate these forms. For this purpose the form-genera *Æcidium*, *Cæoma*, *Peridermium*, *Ræstelia* and *Uredo* are recognized. We group these under the heading **Uredinales Imperfecti**.

Darluca and *Tuberculina*, two imperfect fungi, are often found growing as parasites upon the rust fungi.

KEY TO FAMILIES OF **Uredinales**

- | | |
|---|---|
| Teliospores in germination becoming
4-celled, compacted laterally
into waxy layers; walls of the
spores weakly gelatinous..... | 1. Coleosporiaceæ p. 241. |
| Teliospores germinating by a promy-
celium | |
| Teliospores compacted laterally
into a crust or column (rarely
solitary within the tissues);
walls of the spores firm..... | 2. Melamsporaceæ , p. 245. |
| Teliospores free or fascicled; walls
of the spores firm or with an
outer hygroscopic layer..... | 3. Pucciniaceæ , p. 254. |
| Teliospores unknown..... | 4. Uredinales Imperfecti , p. 278. |

Coleosporiaceæ

Teliospores united in a one or two-layered, waxy cushion, sessile or borne on a broad sac-like stalk and then at the beginning 2-celled. Each original spore-cell divides to four super-imposed cells from each of which a simple sterigma emerges. This bears a large basidiospore.

The most important character is the peculiar mode of basidiospore production, the 4-celled promycelium being formed within the spore.

Coleosporium Léviellé

Basidiospore ellipsoid, teliospores in a single layer in a flat crust.

O. *Pycnia* flattish, linear, dehiscent by a slit, without ostiolar filaments.

I(= *Peridermium*). *Æcia* erumpent, definite; peridium colorless with verrucose walls; spores globose to oblong, with colorless walls, the outer part formed of densely packed, deciduous tubercles.

II. *Uredinia* erumpent, definite, without peridium; spores catenulate, globoid to oblong, pulverulent; wall colorless, closely verrucose, pores obscure.

III. Telia indehiscent except through weathering, waxy, somewhat indefinite, usually roundish; spores sessile, 1-celled (by early division of the contents appearing 4-celled); wall smooth, colorless, thickened and gelatinous at apex.

The genus is usually heteroecious. Arthur lists some twenty-four species for America.

There are many biologic forms, morphologically indistinguishable yet not inter-inoculable. The æcial stage is found on leaves of conifers, the telia on a large variety of hosts.

C. ipomœæ (Schw.) Burr.^{1, 2}

O. Pycnia amphigenous, scattered or gregarious in rows, olivaceous-black, averaging 0.24×0.41 mm.

I (= Peridermium ipomœæ). Æcia flattened laterally, usually in a single row, averaging 0.4×1.6 mm.; peridial cells ovoid to elliptic or rhomboid in face view, mostly overlapping, averaging $21 \times 41 \mu$, with walls $2-5 \mu$ thick, the inner closely and finely verrucose; æciospores ovoid to ellipsoid, $16-20 \times 22-27 \mu$, walls colorless and verrucose with somewhat deciduous tubercles $1-2 \mu$ in diameter and $1-3 \mu$ high.

II. Uredinia hypophyllous, widely scattered or somewhat clustered, $0.25-1$ mm. across, early naked, orange-yellow fading to white, ruptured epidermis usually inconspicuous; spores ellipsoid, $13-21 \times 18-27 \mu$, more or less angular and irregular; wall thin, $1-1.5 \mu$, closely and noticeably verrucose.

III. Telia hypophyllous, widely scattered, often confluent, pulvinate, 0.5 mm. or less across, deep reddish-orange fading to pale-yellow; spores with wall swelling $20-40 \mu$ above; contents orange-yellow fading to colorless, oblong, or slightly clavate, $19-23 \times 60-80 \mu$, rounded or obtuse at both ends.

Common on various Ipomœas and their kin, among them morning glory and sweet potato.

Æcia on *Pinus echinata* and various other pines.

C. solidaginis (Schw.) Thüm.

O. Pycnia amphigenous, scattered, numerous, originating between mesophyll and cortical layer, noticeable, $0.3-0.5$ mm. wide by $0.5-0.8$ mm. long, dehiscent by a longitudinal slit, low-conoidal, $80-100 \mu$ high.

¹ Hedgcock, George G. & Hunt, N. Rex. New species of *Peridermium*. *Mycol.* **9**: 239, 1917.

² Hedgcock, George G. & Hunt, N. Rex. Notes on species of *Coleosporium*—II. *Mycologia* **14**: 297, 1922.

I (= *Peridermium acicolum*). *Æcia* from a limited mycelium, amphigenous, numerous, scattered on discolored spots occupying part of a leaf, erumpent from longitudinal slits, tongue-shaped, 0.5–1 mm. long by 0.5–0.7 mm. high; peridium rupturing irregularly, moderately firm, white, cells overlapping, 35–45 μ long, not much narrower, walls transversely striate, inner coarsely verrucose, thick, 5–6 μ , outer less rough and somewhat thinner; spores ellipsoid, 20–25 x 28–40 μ ; wall colorless, closely and coarsely verrucose with deciduous tubercles which are directed away from a smooth spot extending up one side, thick, 2–3 μ on the smooth spot, increasing to 5–6 μ on the opposite side, including the tubercles.

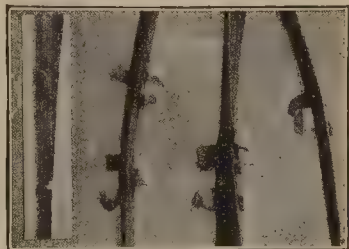


FIG. 247.—Stages O. and I. of *Coleosporium solidaginis* (*Peridermium*) on *Pinus rigida*. After Clinton.

II. Uredinia hypophyllous, rarely also epiphyllous, irregularly scattered, or at first somewhat gregarious and crowded, 0.3–0.5 mm. across, soon naked, yellow or orange-yellow, ruptured epidermis inconspicuous; spores ellipsoid or globoid, 17–22 x 20–30 μ ; wall rather thin, 1–2 μ , closely and strongly verrucose; contents orange-yellow when fresh, fading to colorless.

III. Telia hypophyllous, scattered irregularly or sometimes crowded and confluent, slightly elevated, 0.3–0.5 mm. across, reddish-orange; spores with wall swelling 30–40 μ thick above; contents orange-yellow fading to colorless, terete, 15–23 x 55–80 μ , rounded or obtuse at both ends; basidiospores globoid or elliptical, about 12x18 μ , orange-yellow.

O and I on fourteen species of pine.

II and III. Uredinia and telia on aster, *Solidago*.

C. senecionis (Schum.) Fries

O. Pycnia amphigenous, scattered, numerous, originating between mesophyll and cortical layer, noticeable, 0.2–0.3 mm. wide, 0.5–1 mm. long, dehiscent by a longitudinal slit, 70–100 μ high.

I (= *Peridermium oblongisporium*). *Æcia* from a limited mycelium, amphigenous, bullate, tongue-shaped, 1–2 mm. long, 0.7–1 mm. high, whitish; peridium rupturing irregularly, fragile, white, cells overlapping, outer and inner walls of same thickness, 3–4 μ , outer smooth, inner moderately verrucose; spores broadly ellipsoid, 17–24 x 28–36 μ , wall colorless, thick, 3–4 μ , densely verrucose with prominent elongate papillæ.

II. Uredinia hypophyllous, thickly scattered, about 0.5 mm. across, early naked, bright orange-yellow fading to pale-yellow, ruptured epidermis evident; spores elliptical-globoid or obovate-globoid, $17-21 \times 20-27 \mu$; wall thin, $1-1.5 \mu$, evenly but not densely verrucose, with low papillæ.



FIG. 248.—*Coleosporium senecionis*, showing germination of teliospores. After Plowright.

III. Telia hypophyllous, scattered, often confluent, small, 0.3 mm. across, brilliant orange yellow fading to pale orange yellow; spores with wall swelling $15-25 \mu$ thick above; contents orange yellow fading to pale yellow, clavate or clavate-oblong, $16-20 \times 60-83 \mu$, rounded at both ends or narrowed below.

I. *Æcia* on *Pinus sylvestris*.

II and III. Uredinia and telia on *Senecio*. What may be this same fungus is reported also on cultivated *Cineraria*. The teliospores hiber-

nate in their dark-red sori producing promycelia in the spring. The sporidia bring about spring infection of the pine leaves and young twigs, later resulting in pycnia and *æcia*.

C. pini Gall.

O. Pycnia unknown, probably wanting.

III. Telia amphigenous, on yellow spots, usually near the tips of the leaves, long covered by the epidermis, 1-5 mm. long, or when confluent up to 10 mm. or more, reddish-orange fading to pale-yellow or dirty-white, ruptured epidermis inconspicuous; teliospores with walls swelling $30-50 \mu$ above, and soon disappearing upon exposure; contents orange-yellow fading to nearly colorless, clavate, slender, $13-20 \times 60-100 \mu$, acute or rounded above, much narrowed below, sides wavy or irregular.

This is set apart by Arthur as the type of a distinct genus, *Gallowaya*, based on the absence of spore forms other than the teliospores.

It causes serious leaf loss on *Pinus virginiana*.

C. campanulæ (Pers.) Lév.

O. Pycnia amphigenous, scattered, numerous, originating between mesophyll and cortical layer, noticeable, large, 0.2-0.4 mm. wide, 1-2 mm. long, dehiscent by a longitudinal slit, $90-110 \mu$ high.

I (= *Peridermium rostrupi*). *Æcia* from a limited mycelium, amphigenous, scattered, 1-3 on discolored spots, bullate, tongue-shaped, large, 1-3 mm. long, 0.7-1.5 mm. high, yellow fading to

white; peridium rupturing irregularly, fragile, white, cells overlapping, outer and inner walls same thickness, about 4–6 μ , outer smooth, inner moderately verrucose; spores broadly ellipsoid or globose, 17–22 x 22–31 μ ; wall colorless, thin, 2–3.5 μ , densely verrucose, with prominent, elongate papillae.

II. Uredinia hypophyllous, scattered, often confluent, 0.5–1 mm. across, soon naked, orange-red fading to white, ruptured epidermis evident; spores ellipsoid, 18–23 x 20–30 μ ; wall thin, 1–1.5 μ , densely verrucose with prominent, elongate papillae.

III. Telia hypophyllous, scattered, often confluent, small, 0.2–0.5 mm. across, slightly elevated, blood-red fading to pale brownish-yellow; spores with wall swelling 15–25 μ thick above; contents orange-red fading to nearly colorless, cylindrical or clavate-oblong, 17–24 x 55–85 μ , rounded or obtuse at each end.

O and I on *Pinus rigida*.

II and III on *Campanula* and kin.

There are numerous other species of less importance.

Melampsoraceæ (p. 241)

Telia forming a more or less definite crust or column; teliospores compacted laterally into layers or rarely solitary in the tissues, sessile; wall firm or rarely with a gelatinous layer.

The family is of importance economically chiefly as the cause of flax rust and on pine, causing the blister rust; its uredinial and telial stages also do slight injury on poplars and willows.

KEY TO GENERA OF **Melampsoraceæ**

Telia indehiscent

Sori all subcuticular; teliospores compacted in dense layers to form a crust; æcia when present without a peridium; uredinia when present with delicate, cellular peridium with peripheral, free or imbricated paraphyses or neither.

Teliospores in a single layer; uredinia with spores and paraphyses intermixed.

1. **Melampsora**, p. 246.

Teliospores in more than one layer; uredinia with peridium or paraphyses or neither.

2. **Phakopsora**, p. 248.

- Pycnia* subcuticular, other sori subepidermal, or the telia within the epidermal cells or between the mesophyll cells; uredinia when present with a peridium
- Teliospores approximately in a single layer within or beneath the epidermis; urediniospores globoid to oblong
- Walls of the teliospores colored; urediniospores echinulate throughout..... 3. *Pucciniastrum*, p. 248.
- Walls of the teliospores colorless; urediniospores echinulate..... 4. *Melampsorella*, p. 250.
- Telia erumpent, sori all subepidermal
- Telia velvety..... 5. *Kuehneola*, p. 251.
- Telia waxy; teliospores often firmly united sidewise and endwise, adhering and extruded in long columns; æcia when present with inflated peridium, dehiscence circumscissile; uredinia when present with peridium, spores borne singly on pedicels. Teliospores 1-celled..... 6. *Cronartium*, p. 251.

Melampsora Castaigne (p. 245)

O. *Pycnia* half spherical.

I. *Æcia* of *caoma*-type, no peridium or paraphyses.

II. Urediniospores solitary, membrane colorless.

III. Teliospores 1-celled, rarely more, in flat irregularly limited crusts. Basidiospores spherical.

The question of biologic specialization is especially complicated in this genus. The uredinal and telial stages occur in abundance on willows and poplars, the æcial stage on a wide range of plants embracing gymnosperms, monocotyledons and dicotyledons.

M. lini DC.

O. *Pycnia* amphigenous, numerous, scattered, inconspicuous, subepidermal, pale-yellow, flattened globoid or lens-shaped, 100–175 μ in diameter, 65–95 μ high; spores ellipsoid, 2–3 x 3–4 μ .

I. *Æcia* chiefly hypophyllous, numerous, scattered, rounded, 0.2–0.4 mm. across, bright orange-yellow, conspicuous, formed between epidermis and mesophyll, soon naked, ruptured epidermis evident; spores globoid, 19–27 x 21–28 μ .; wall colorless, thin, about

1 μ , finely and evenly verrucose, with distinct papillæ, pores not evident.

II. Uredinia amphigenous and cauliculous, scattered or somewhat gregarious, often crowded, round or on stems elongate, 0.3–0.5 mm. across, soon naked, reddish-yellow fading to nearly white, pulverulent, ruptured epidermis noticeable; spores broadly elliptical or obovate, 13–18 x 15–25 μ , wall colorless, rather thin, 2 μ , evenly and finely verrucose, with low papillæ, pores equatorial, obscure; paraphyses intermixed with the spores, capitate, large, 5–22 x 40–65 μ , smooth, wall thick.

III. Telia amphigenous and cauliculous, scattered, often confluent, round or elongate, 0.2–0.5 mm. across, slightly elevated, reddish-brown becoming blackish; spores subepidermal, appressed into a single layer, prismatic, 1-celled, 10–20 x 42–50 μ ; wall brown, smooth, thin, about 1 μ , not thickened above.

Autœcious on flax. Sometimes injurious.

M. medusæ Thüm.

O. Pycnia chiefly epiphyllous, scattered or somewhat gregarious, minute, punctiform, pale-yellow, inconspicuous, subcuticular, hemispherical, 40–80 μ in diameter, half as high.

I. Æcia chiefly hypophyllous, scattered or somewhat gregarious, small, 0.1–0.3 mm. broad, round or oblong, pale-yellow fading to white, inconspicuous, formed between epidermis and mesophyll, soon naked, pulverulent, ruptured epidermis noticeable; æciospores globoid, 17–22 x 17–24 μ ; wall colorless, thick, 2.5–3 μ , finely verrucose, with minute crowded papillæ, pores indistinct.

II. Uredinia amphigenous, or only hypophyllous, scattered, roundish, small, 0.2–0.4 mm. across, early naked, somewhat pulverulent, orange-yellow, fading to pale brownish-yellow, ruptured epidermis usually inconspicuous; urediniospores ellipsoid or obovate-ellipsoid, 15–18 x 22–30 μ , usually flattened laterally; wall colorless, 2.5–3 μ or up to 10 μ on the flattened sides, sparsely and evenly verrucose with fine papillæ, except on the flattened sides which are smooth; paraphyses numerous, intermixed with the spores, capitate, smooth, 40–65 μ long, head 14–25 μ broad, wall thick, 3–6 μ , peripheral paraphyses thinner-walled and more clavate.

III. Telia amphigenous or only hypophyllous, scattered or somewhat confluent, irregularly roundish, small, 0.2–0.4 mm. across, slightly elevated, light reddish-brown, becoming deep

chocolate-brown, subepidermal; teliospores prismatic, 12–15 x 30–45 μ ; wall smooth, cinnamon-brown, uniformly thin, 1 μ .

O and I on larch, II and III on poplar. Common on all species of *Populus* and often doing serious damage by its early defoliation of the trees.

Eight other species are recorded with the stage II, III on *Salix*, 8 on *Populus*; three of these have the stage I on *Larix*; others are on *Allium*, *Ribes*, *Tsuga*, etc.

M. saliciscapræ (Pers.) Wint.: is injurious on willow.

Phakopsora Dietel (p. 245)

Cycle of development imperfectly known; only uredinia and telia recognized, both subepidermal. Uredinia erumpent, definite, roundish, pulverulent, with delicate cellular peridium, with peripheral free or imbricated paraphyses or neither. Urediniospores sessile, apparently produced in chains with one spore maturing at a time and falling away before the next one enlarges, obovate-globose or ellipsoid; wall pale-yellow, echinulate or rarely verrucose, pores obscure. Telia indehiscent, forming lenticular masses, two or more cells thick at center. Teliospores 1-celled; walls smooth.

P. vitis (Thüm.) Syd.

II. Uredinia hypophyllous, scattered thickly over wide areas, round, minute, 0.1 mm. or less across, soon naked, arising between epidermis and mesophyll, surrounded by numerous incurved paraphyses, pulverulent, pale-yellow, fading to dirty white, ruptured epidermis inconspicuous; urediniospores broadly ellipsoid or obovate, 13–17 x 18–27 μ ; wall nearly colorless, thin, 1 μ , minutely and rather closely echinulate, pores obscure; paraphyses hyphoid, curved and irregular, 6–10 μ thick, 30–60 μ long, wall uniformly thin, 1 μ , yellowish.

III. Telia hypophyllous, scattered thickly over large areas, roundish, minute, 0.1–0.2 mm. across, indehiscent, 3–4 cells thick; teliospores ovoid, 12–15 x 20–30 μ , wall smooth, nearly colorless, thin, 1 μ or less.

On grape leaves in Southern United States and West Indies. Also in South America and Japan.

Pucciniastrum Otth. (p. 246)

Heteroecious. The cycle of development includes pycnia, æcia uredinia and telia, with distinct alternating phases.

O. *Pycnia* subcuticular, low-conoidal, without ostiolar filaments.

I. *Æcia* erumpent, cylindrical. Peridium delicate, verrucose on inner surface. Spores ellipsoid, verrucose except one side which is thinner and smooth.

II. Uredinia barely protruding through the epidermis, dehiscient by a central pore. Peridium hemispherical, delicate, cells longer at orifice. Spores borne singly on pedicels, obovate to ellipsoid; wall colorless, echinulate, pores indistinct.

III. Telia indehiscent, forming more or less evident layers in the epidermal cells or immediately beneath the epidermis. Spores oblong or prismatic, 2 to 4-celled by vertical partitions in two planes; wall smooth, colored.

P. hydrangæ (B. & C.) Arth.

O and I. Unknown.

II. Uredinia hypophyllous, scattered, round, small, 0.1–0.2 mm. across, dark-yellow fading to pale-yellow, ruptured epidermis inconspicuous, dehiscient by a central pore; peridium hemispherical, delicate, cells small, cuboid, walls uniformly thin, 1–1.5 μ , ostiolar cells slightly or not elongate, 10–16 μ , barely pointed, walls thin, smooth; spores broadly elliptical or obovate, 12–18 x 16–24 μ ; wall nearly colorless, thin, 1–1.5 μ , sparsely and strongly echinulate.

III. Telia amphigenous or chiefly epiphyllous, effused or confluent into small angular groups, 0.3–0.8 mm. across, not raised, reddish-brown; spores forming a single layer within the epidermal cells or sometimes between the epidermis and mesophyll, globose, 22–28 x 24–28 μ , wall dark cinnamon-brown, uniformly thin, 1.5–2 μ .

It is found in the uredinal and telial stages on *Hydrangea* on which it may be quite serious.

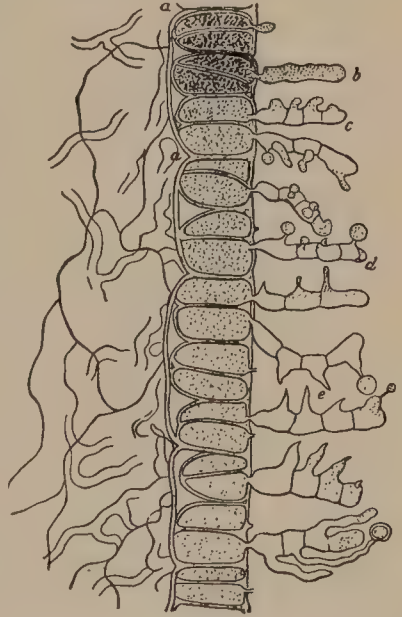


FIG. 249.—*Pucciniastrum* showing germinating teliospores. After Hartig.

Melampsorella Schröter (p. 246)

O. Pycnia hemispherical, without ostiolar filaments.

I. *Æcia* erumpent, definite, oblong, bullate; peridium colorless, with thin-walled cells; æciospores ellipsoid; wall colorless, thin, verrucose, without smooth spot.

II. Uredinia barely protruding through the epidermis, dehiscent by a central pore; peridium hemispherical, delicate, cells slightly or not enlarged at orifice; urediniospores borne singly on pedicels, obovate to ellipsoid; wall slightly colored, echinulate, pores obscure.

III. Telia effused, indehiscent; teliospores globoid to ellipsoid, 1-celled; wall smooth, colorless, thin.

M. elatina (A. & S.) Arth.

O. Pycnia epiphyllous, few, scattered, punctiform, inconspicuous, subcuticular, not extending far into walls of epidermis, depressed-hemispherical, small, 100–130 μ broad, 40–50 μ high.

I. *Æcia* from a perennial mycelium, dwarfing the young shoots and forming witches' brooms, hypophyllous, forming two irregular lines, deep-seated, wholly dropping out of the substratum at maturity, roundish or irregularly oblong, large, 0.5–1 mm. across, bladdery, soon open by falling away of the upper part; peridium colorless, dehiscence irregular, cells with thin inner and outer walls; æciospores broadly ellipsoid or nearly globoid, 14–18 x 16–28 μ ; wall colorless, thin, 1–1.5 μ , closely and rather finely verrucose.

II. Uredinia amphigenous, scattered or somewhat grouped, small, round, 0.1–0.4 mm. across, orange-red when fresh, pale yellow when dry; peridium hemispherical, dehiscent by a small central orifice, cells elongate at sides, polygonal above, inner and outer walls same thickness; urediniospores ellipsoid or obovoid, 12–18 x 16–30 μ ; walls pale yellow, rather thin, 1–1.5 μ ; sparsely echinulate with short conical points.

III. Telia hypophyllous, on whitish or pale reddish spots; teliospores within the epidermal cells, 1-celled, short-cylindrical or polygonal, 13–20 μ broad; wall colorless, smooth, thin.

I (= *Peridermium elatinum*) on fir causing swelling, cankers and witches' brooms.

II and III on various members of the pink family.

All stages possess perennating mycelium. The æcial stage is of most economic significance, producing witches' brooms of various

sizes. The æcia are formed only on the deformed needles of the witches' brooms.

Kuehneola Magnus (p. 246)

Æcia wanting; uredinia pulvinate, telia similar to *Phragmidium* but with smooth spores with the germ pores apical.

K. uredinis (Lk.) Arth.

II (= *Uredo muelleri*). Uredinia lemon-yellow, minute dots; spores globose to elliptic, about $26\ \mu$, hyaline, slightly verrucose.

III. Telia solitary, pale, $250\text{--}500\ \mu$ broad; spores 5 to 6 to 12-celled, episore hyaline, cells $17\text{--}47 \times 15\text{--}26\ \mu$; basidiospores $8.5\text{--}9.5\ \mu$.

The telia are pale yellowish-white, thus readily distinguishing them from other *Rubus* rusts.

The uredinia are common and sometimes injurious on *Rubus*. The sori are small and scattered.

Cronartium Fries (p. 246)

O. Pycnia deep-seated, broad and flat.

I (= *Peridermium*). Æcia erumpent, inflated; peridium membranous, rupturing at the sides rather than above, 2–4 cells thick, outer surface smooth, inner verrucose. Spores ellipsoid; wall colorless, coarsely verrucose with deciduous tubercles, except a smooth spot on one side.

II. Uredinia somewhat erumpent; peridium moderately firm, rupturing above, upper part evanescent; peridial cells isodiametric; spores borne singly on pedicels, globoid to ellipsoid; wall nearly or quite colorless, echinulate, pores obscure.

III. Telia erumpent, at first arising from the uredinia, the catenulate spores adhering to form a much extended, cylindrical or filiform column, horny when dry; spores oblong to fusiform, 1-celled; wall slightly colored, thin, smooth.

All known æcial stages are *Peridermiums* on stems of conifers.

C. ribicola F. de Wal.

O. Pycnia caulicolous, scattered, honey-yellow, forming minute, bladdery swellings. Spores hyaline, ovoid to elliptical, $1.9\text{--}4.7\ \mu$.

I (= *Peridermium strobis*). Æcia caulicolous, causing fusiform swellings of the stem, rounded to elongate; peridium inflated, rupturing at sides, thick, membranous; spores ellipsoid to ovoid,

18–20 x 22–23 μ , wall colorless, coarsely verrucose except on elongate smooth spot, 2–2.5 μ thick, on smooth spot 3–3.5 μ thick.

II. Uredinia hypophyllous, thickly scattered in groups, round, pustular, 0.1–0.3 mm., at first bright yellow; peridia delicate;

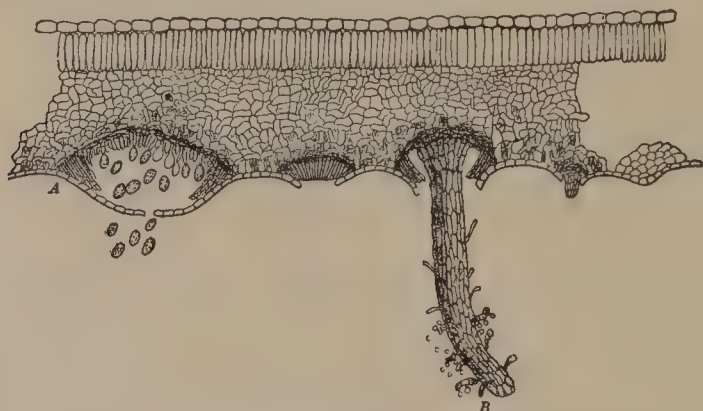


FIG. 250.—*Cronartium*. A, uredinium; B, telium. After Tubeuf.

spores ellipsoid to obovate, 14–22 x 19–35 μ , wall colorless, 2–3 μ thick, sparsely and sharply echinulate.

III. Telial columns hypophyllous, cylindrical, 125–150 μ thick, up to 2 mm. long, curved, bright orange-yellow becoming brownish; spores oblong or cylindrical, 8–12 x 30–60 μ ; wall nearly colorless, smooth, rather thick, 2–3 μ .

Heteroecious O, I, on white pine, *Pinus cembra* and several other 5-leaved species; II and III on currant and gooseberry and several other species of *Ribes*.

The telial stage was first noted in Geneva, N. Y., in 1906, though the rust has been known in Europe since 1854. Its effects are most serious in its æcial stage, though the telial stage is very abundant and conspicuous. The generic connections of the forms was proved by Klebahn in 1888 by inoculations.

The mycelium is doubtfully perennial in *Ribes* and certainly is perennial in the bark of the pine.

C. comptoniæ Arth.

I (= *Peridermium pyriforme*) on *Pinus* trunks. III on *Comptonia*.

The *Peridermium* is perennial in the trunks of the pine where it does considerable injury.

C. filamentosum (Pk.) Hedg. (= *Peridermium filamentosum* Pk.) is the most destructive *Peridermium* on pine in the West. The alternate stage is on *Castilleja*.

C. cerebrum (Pk.) H. & L.

Heteroecious; I (= *Peridermium cerebrum*) on pine, III on oak.

Globoid swellings 5–25 cm. across are formed on pine trees.



FIG. 251.— *Cronartium comptoniae* (*Peridermium*) on *Pinus*.
After Clinton.

C. occidentale Hedgcock, Bethel & Hunt.¹

O and I on *Pinus edulis* and *P. monophylla*.

II and III on *Ribes* spp. and *Grossularia* spp.

This Rocky Mountain rust in its uredinial and telial stages is quite similar to *C. ribicola* with which it has been confused in the past. It is only known to attack one- and two-needled pines and does not affect the five-needled pines.

C. pyriforme (Pk.) Hedgcock and Long.²

I on *Pinus* spp.

II and III on *Comandra* spp.

This rust is widely distributed over the United States attacking in its aëcial form two- and three-needled pines. It produces cankers

¹ Hedgcock, George G., Bethel, Ellsworth, and Hunt, N. Rex. Piñon blister-rust. Jour. Agr. Res. **14**: 411, 1918.

² Hedgcock, G. G. and Long, W. H. A disease of pines caused by *Cronartium pyriforme*. U. S. Dept. Agr. Bur. Pl. Ind. Bul. 247, 1915.

and slight fusiform swellings which usually encircle the trunks, in young trees, killing the cambium and thus leading to the destruction of the tree.

Pucciniaceæ (p. 241)

Teliospores stalked, stalk sometimes short or evanescent, 1-celled or with several cells in a row or several united to form a parasol-like head on a compound stalk; separate or gelatinous-embedded; basidiospores formed from promycelia. *Æcia* with or without peridia; urediniospores solitary.

This is the largest and most important family of the order, infesting numerous valuable agricultural plants and causing enormous loss. The species are manifold and the complexities, owing to polymorphism, heterœcism and biologic specialization, are very great.

KEY TO GENERA OF Pucciniaceæ

- Teliospores free, 2-8 at apex of a common stalk; all spore forms present 1. **Tranzschelia**, p. 255.
- Teliospores not borne on a common pedicel
 - Teliospore wall without gelatinous layer
 - Pycnia* subcuticular, other sori subepidermal; *æcia* when present without peridium; uredinia when present without peridium, but usually with encircling paraphyses
 - Teliospores mostly tuberculate, the pores more than one and lateral, with more than three cells lineally arranged 2. **Phragmidium**, p. 256.
 - Teliospores 2-celled, mostly smooth, the pores one in a cell and apical 3. **Gymnoconia**, p. 257.
 - Sori all subepidermal; *æcia* when present with a peridium; uredinia when present with no peridium or rarely with encircling paraphyses
 - Teliospores embedded in a more or less gelatinous matrix 4. **Gymnosporangium**, p. 258.

Teliospores not embedded in a gelatinous matrix, dark colored

Teliospores 1-celled 5. *Uromyces*, p. 265.

Teliospores 2-celled 6. *Puccinia*, p. 268.

Tranzschelia Arthur (p. 254)

Cycle of development includes pycnia, æcia, uredinia and telia, with alternating phases; autœcious or heterœcious; pycnia subcuticular, other sori subepidermal.

O. I. Pycnia depressed-conical or hemispherical; hymenium flat; æcia erumpent, cylindrical; peridium dehiscient at apex, becoming recurved. Æciospores globoid; wall colored, finely verrucose.

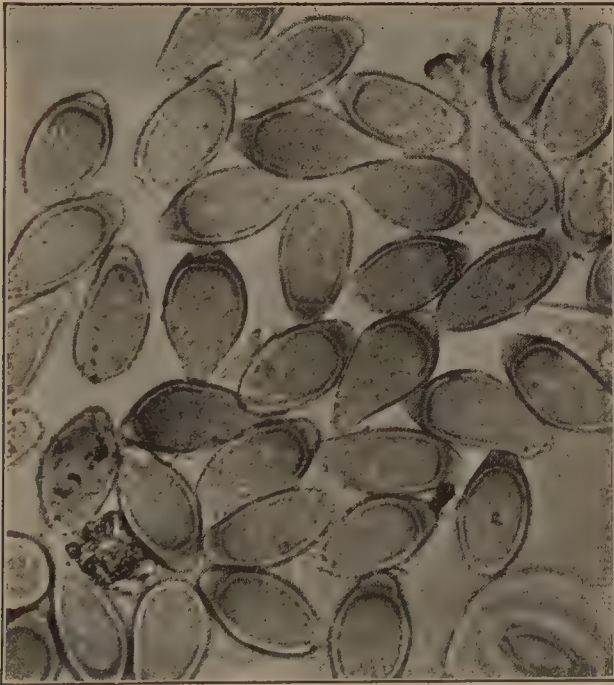


FIG. 252—*T. punctata*, urediniospores. After Holway.

II. Uredinia erumpent, definite, without peridium; urediniospores borne singly on pedicels, with paraphyses intermixed, obovoid, somewhat narrowed at both ends; wall colored, usually paler below, echinulate; pores equatorial.

III. Telia erumpent, definite, pulverulent, without peridium; teliospores forming heads or balls by being attached by short,

fragile pedicels to a common stalk, which is short and inconspicuous, 2-celled by transverse septum, cells rounded and easily falling apart, wall colored, verrucose.

T. punctata (Pers.) Arth.

I (= *Æcidium punctatum*). *Æcia* uniformly scattered over the leaf, hypophyllous, flat, semi-immersed, with torn yellowish edges; spores subglobose, pale yellowish-brown, 15–24 μ in diameter; pycnia scattered, blackish, punctiform.

II. Uredinia light-brown, small, round, crowded, pulverulent, often confluent; spores ovate or subpyriform, apex darker, thickened, bluntly conical, closely echinulate, brown, 20–35 x 12–16 μ , mixed with numerous capitate brownish paraphyses.

III. Telia pulverulent, dark-brown, almost black; spores consisting of two spherical cells, flattened at their point of union, the lower cell often being smaller and paler; episporium uniformly thick, chestnut-brown, thickly studded with short stout spines. Spores 30–45 x 17–25 μ ; pedicels short, colorless.

Heteroecious: O and I on *Hepatica*, *Thalictrum* and *Anemone*.

II and III on *Prunus* spp., peach, almond, plum, cherry, apricot.

The æcial stage is perennial. Urediniospores have also been shown to remain viable over winter. The peculiar character of the urediniospores has sometimes led this fungus to be mistaken for a *Uromyces*.

Phragmidium Link (p. 254)

O. Pycnia present.

I. *Æciospores* in basipetal chains. The first two spore forms

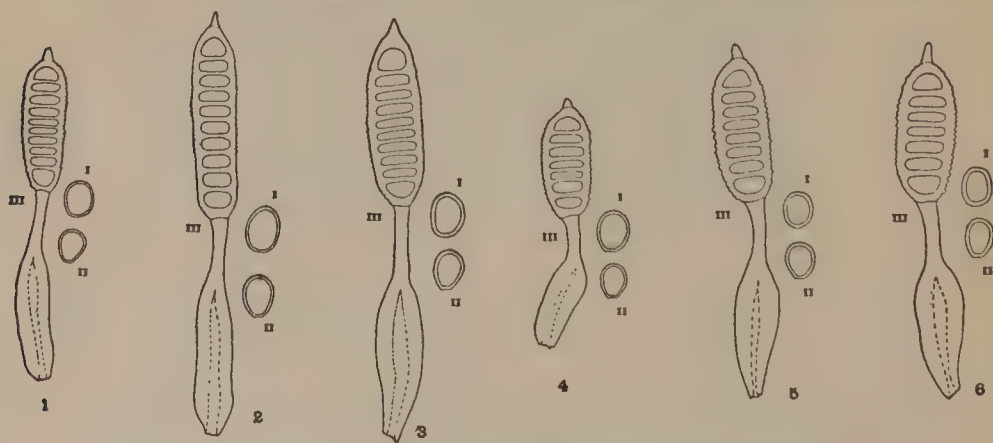


FIG. 253.—Uredinio- and teliospores of: 1. *P. americanum*; 2. *P. rosæ-setigeræ*; 3. *P. rosæ-californicæ*; 4. *P. rosæ-arkansanæ*; 5. *P. montivagum*; 6. *P. disciflorum*. After Arthur.

are in pulverulent sori, surrounded by clavate or capitate, hyaline paraphyses.

II. Urediniospores single.

III. Teliospores separate, pedicellate, consisting of from three to ten superimposed cells, the uppermost of which has a single apical germ pore, the others about four each, placed laterally.

The æcial stage is a Cæoma, but with a border of incurved paraphyses. The unicellular urediniospores are similarly surrounded, and bear numerous germ pores. The genus is limited to rosaceous hosts and its species are autœcious.

Eight American forms are recognized by Arthur on roses.

Gymnoconia Lagerheim (p. 254)

O. *Pycnia conic*.

I (=Cæoma) peridia and paraphyses none.

III. Spores as in *Puccinia*.

This genus bears a superficial resemblance to *Puccinia* but is easily distinguished by its naked æcial sori.

G. interstitialis (Schl.) Lag.¹

O. *Pycnia glandular*, numerous, mostly epiphyllous.

I (=Cæoma *nitens*) hypophyllous, sori irregular, confluent; spores orange-red, globose to elliptic, epispore thin, 18–35 x 12–24 μ .

III. Telia hypophyllous, few, sparse, cinnamon-brown; spores more or less angular, 36–45 x 22–27 μ , pedicel short or wanting.

Autœcious on raspberries, wild and cultivated.

The pycnial stage appears first in spring giving to the leaves and stems a glandular appearance. About two or three weeks later the æcial stage is visible on the lower surface of the leaves; the epidermis soon ruptures and the orange beds of spores show. The pycnia are then fully developed. The affected plants are much stunted and unproductive, but are not killed. The fungous mycelium is intercellular, growing rapidly into formative tissues and perennating in the woody shoots. The knob-like haustoria penetrate the cells and often lie against the nuclei. The mycelium is especially abundant in the pith near the bundles.

¹ Kunkel, L. P. The production of a promycelium by the æcidiospores of *Cæoma nitens*. *Bul. Torr. Bot. Cl.* **40**: 361; also, Nuclear behavior in the promycelia of *Cæoma nitens* Burrill & *Puccinia peckiana* Hawes, *Amer. Jour. Bot.* **1**: 37, 1914; same author, Further studies of the orange rusts of *Rubus* in the United States. *Bul. Torr. Bot. Cl.* **43**: 559, 1916; same author, Further data on the orange rusts of *Rubus*. *Jour. Agr. Res.* **19**: 501, 1920.

The æciospores may germinate at once and infect susceptible hosts. The teliospore which is less conspicuous and therefore rarely seen is of the Puccinia type. The telia appear in July and August, usually hypophyllous, and the sori are very small and inconspicuous.

A second form of this rust, almost indistinguishable from the first, occurs on wild and cultivated blackberries; the chief differ-

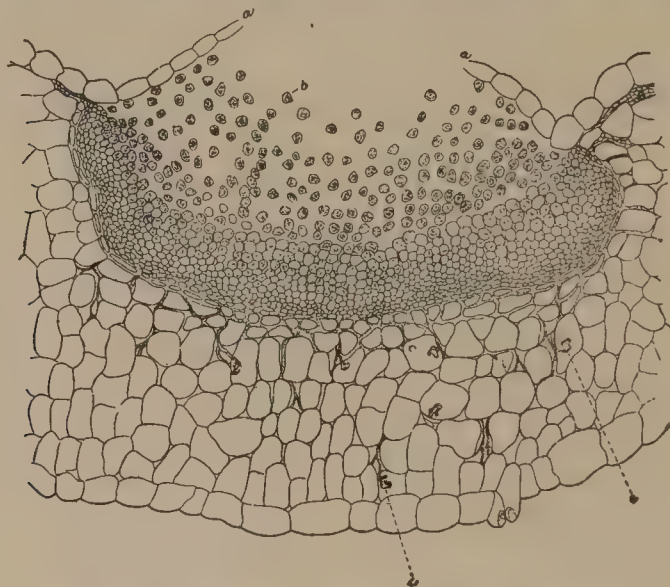


FIG. 254.—*G. interstitialis*, caoma sorus. After Newcomb.

ence rests in the manner of germination of the spores, which in the second form produce promycelia, hence functioning as teliospores, while those of the other form produce germ tubes. Owing to this fundamental difference in germination, constituting one form as a short cycle rust, together with very slight difference in color and size of the spores, this second form is regarded by some as a distinct species belonging in a separate genus, *Kunkelia*.

Gymnosporangium Hedwig ^{1, 2} (p. 254)

Cycle of development including pycnia, æcia and telia, with distinct alternating phases; heteroecious and autoecious. Pycnia and other sori subepidermal.

¹ Kern, F. D. A biological and taxonomic study of the genus *Gymnosporangium*. Bul. N. Y. Bot. Gard. 7: 391, 1911.

² Sydow. Monog. Ured. 1915.

O. Pycnia deep-seated, usually globoid, generally prominent and conspicuous, at first honey yellow, usually becoming blackish, globose or flattened-globose, with ostiolar filaments.

I (=Röestelia) erumpent, at first cylindric. Peridium dingy white, usually elongated into a tubular form, membranous, tending to rupture by longitudinal slits along the sides; peridial cells imbricate and often articulated, occasionally hygroscopic, outer walls smooth, rather thin, inner walls smooth, verruculose, verrucose, rugose, or spinulose. Æciospores in basipetal chains with alternate barren cells, inclosed in a peridium, globoid to broadly ellipsoid; wall colored, verrucose, usually with numerous, scattered, evident germ pores.

III. Telia erumpent, naked, usually definite, variously shaped, gelatinous and elastic at maturity, expanding considerably when



FIG. 255.—Gymnosporangium, spore masses just emerging. After Heald.

moistened. Teliospores chiefly 2-celled, in some species 3, 4, or 5-celled, by transverse septa; walls colored, of various thickness, smooth; pores usually two in each cell, sometimes, 1, 3, or 4, variously arranged; pedicels hyaline, elastic, usually of considerable length, cylindric, rarely carotiform, walls thick, the outer portion swelling and becoming gelatinous to form a jelly-like matrix in which the spores appear embedded.

All of the species agree in possessing the same spore forms, pycnia, æcia, and telia which appear in the same sequence in the

different species; also in the fact, with two exceptions, that the æcia grow on pomaceous plants, and the telia on *Juniperus* (with few exceptions).

The æciospores are borne in æcia which rest in orange or yellow spots often strongly thickened. Pycnia abound. The æcium

with its thick peridium is erumpent and projects to some distance above the host surface, this character giving rise to the separate form-genus, *Ræstelia*. The peridial margin which may be lacerate or fimbriate is used in specific characterization. The spores are borne and function as in ordinary æcia. They bear several germ pores.

Æciospores germinate at once and if they fall upon suitable coniferous hosts bring about infection. The mycelium penetrating the leaf or branch often induces large hypertrophy.

In spring in moist weather the teliospores are found in spore masses composed of the spores,

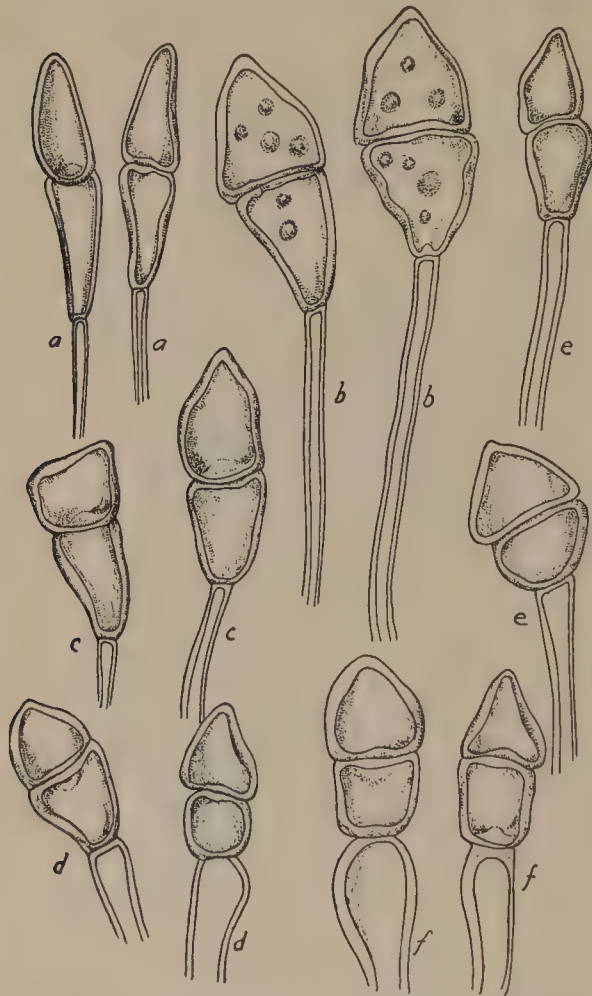


FIG. 256.—*Gymnosporangium* teliospores. *a*, *G. clavariæ* forme; *b*, *G. globosum*; *c*, *G. macropus*; *d*, *G. nidus-avis*; *e*, *G. nelsoni*; *f*, *G. clavipes*. After King.

which are usually orange or yellow, and of their long gelatinous pedicels.

Each cell bears one or more germ pores through one of which the tube emerges.

The teliospores germinate immediately *in situ* by typical 4-celled promycelia and four basidiospores are produced on each promycelium.

The basidiospores are capable of infecting only the appropriate alternate host and that when the parts are still young and tender.

The various species usually make good subjects with which to study infection. The teliospore masses placed in water soon become covered with basidiospores. Suspensions of these in water applied to susceptible hosts usually give positive results readily.

G. juniperi-virginianæ Schw. (= *G. macropus*) Link.

O. *Pycnia epiphyllous*.

I. *Æcia* (= *Ræstelia pyrata*) chiefly hypophyllous, usually in annular groups, on thickened discolored spots, at first cylindric, 0.1–0.4 mm. in diameter; peridium splitting extremely early, becoming fimbriate to the base, strongly revolute; peridial cells usually seen only in side view, long and narrow, 10–16 x 65–100 μ , becoming much curved when wet, inner and side walls rather sparsely rugose with ridges extending half way across the side walls; æciospores globoid or broadly ellipsoid, 16–24 x 21–31 μ , wall light chestnut-brown, 2–3 μ thick, finely verrucose.

III. Telia appearing on globoid or reniform galls 5–30 mm. or more in diameter, evenly disposed, cylindric or cylindric-acuminate, 1.5–3 mm. in diameter by 10–20 mm. long, golden-brown; teliospores 2-celled, rhombic-oval or narrowly ellipsoid, 15–21 x 42–65 μ ; slightly or not constricted at the septum; wall pale cinnamon-brown, thin, about 1 μ ; pedicel cylindric, 3–5 μ in diameter; pores two in each cell near the septum.

I. *Æcia* on apple both wild and cultivated.

III. Telia on *Juniperus virginiana* and *J. barbadensis*.

Destructive, particularly in East and South.

Sporidia are matured in twelve to twenty-four hours after the spore-masses expand by moisture, and as soon as the sori begin to dry they are carried away by wind and on suitable hosts infect, through the cell walls, by appresoria. Two or three crops of sporidia may arise in one season but the first crop is largest. Each crop may result in a corresponding crop of æcia. The stage on apple fruits shows as pale yellow spots of pinhead size about seven to ten days after infection. The spots finally become orange colored and in a few weeks the pycnia appear as black specks. On leaves hypophyllous cushions 0.5–1 cm. in diameter form on the spots and bear the æcia, the mature tubes of which are split and

recurved giving a stellate appearance. *Æciospores* pass back to the cedar in summer and cause infection. The mycelium here remains practically dormant until the following spring when the telial galls first become visible. These galls grow throughout the summer, mature in the fall, and give rise to the teliospores during the next spring. The mycelium is thus seen to be biennial.

G. clavariæforme (Jacq.) DC.

I. *Æcia* hypophyllous, fructicolous or caulicolous, usually crowded in small groups 2–3 mm. across on the leaf blades, sometimes in larger groups on the veins, petioles and twigs, often densely aggregated on the fruits and occupying part or all of the surface, cylindric, 0.7–1.5 mm. high by 0.3–0.5 mm. in diameter; peridium soon becoming lacerate, usually to base, erect or spreading; peridial cells long and narrow, often becoming curved when wet, linear in face view, 18–30 x 80–130 μ , linear or linear-oblong in side view, 15–25 μ thick, outer wall 1–2 μ thick, smooth, inner wall and side walls 5–7 μ thick, rather coarsely verrucose with roundish or irregular papillæ of varying sizes; *æciospores* globoid, 21–27 x 25–30 μ , wall light cinnamon-brown, 2.5–3.5 μ thick, moderately verrucose.

III. *Telia* caulicolous, appearing on long, fusiform swellings of various sized branches, numerous, scattered or sometimes aggregated, cylindric, or slightly compressed, 5–10 mm. long by 0.8–1.5 mm. in diameter, acutish, or sometimes forked at the apex, brownish-yellow; teliospores 2-celled, lanceolate, 13–20 x 40–80 μ , occasionally longer, rounded or narrowed above, usually narrowed below, very slightly or not at all constricted at the septum; wall golden-yellow, thin, about 1 μ ; pores 2 in each cell, near the septum.

I. *Æcia* on *Cratægus* spp., *Amelanchier*, *Aronia*, *Cotoneaster*, *Cydonia*, and *Pyrus*.

III. *Telia* on *Juniperus communis*, *J. oxycedrus*, and *J. sibirica*. Spindle-shaped swellings occur on Juniper branches. Cylindric spore-masses ooze through rifts in the bark. *Æciospores* shed in June germinate at once on Juniper twigs and result in the following year in swellings which often later cause death. In spring the spore-masses emerge and the teliospores germinate *in situ*. Upon the rosaceous hosts spots appear eight to fourteen days after infection.

G. globosum Farl.

O. and I. *Æcia* chiefly hypophyllous and crowded irregularly or rarely in approximately annular groups 2–7 mm. across, cylin-

dric, 1.5–3 mm. high by 0.1–0.2 mm. in diameter; peridium soon splitting in the upper part, becoming reticulate half way to base; peridial cells seen in both face and side views, broadly lanceolate in face view, 15–23 x 60–90 μ , linear rhomboid in side view, 13–19 μ thick, outer wall about 1.5 μ thick, smooth, inner and side walls 3–5 μ thick, rather densely rugose with ridge-like papillæ of varying length; æciospores globoid or broadly ellipsoid, 15–19 x 18–25 μ , wall light chestnut-brown, 1.5–2 μ thick, finely verrucose.

III. *Telia* cauliculous, appearing on irregular globoid, gall-like excrescences 3–25 mm. in diameter, unevenly disposed, often separated by the scars of the sori of previous seasons, tongue or wedge-shaped, 1.5–3 mm. broad by 2–5 mm. long at the base and 6–12 mm. high, chestnut-brown; teliospores 2-celled, ellipsoid, 16–21 x 37–48 μ , somewhat narrowed above and below, slightly constricted at the septum; wall pale cinnamon-brown, 1–2 μ thick; pores 2 in each cell, near the septum.

I. *Æcia* on apple, pear, *Cratægus*, mountain ash.

III. *Telia* on *Juniperus virginiana* and *J. barbadensis*. Common and widely distributed in eastern America.

The telial galls are from 0.5 to 2.5 cm. in diameter, very irregular. In late spring dark-brown spore-masses, later yellow-orange, 0.5 to 2.5 cm. long appear.

The *Ræstelia* spots are 0.5–1.0 cm. across. *Pycnia* blackish above. The *æcia* are on thickened hypophyllous spots, long, slender, soon splitting and becoming fimbriate. Mesospores occur occasionally. The æciospores germinate on the cedar. The mycelium stimulates the hosts to extra formation of parenchymatous tissue.

G. juniperinum (L.) Mart.

I. *Æcia* (= *Ræstelia penicillata* [Pers.] Fries.) hypophyllous, in annular or crowded groups, 2–5 mm. across on large, thickened, discolored spots, at first cylindric, 0.5–1.5 mm. high, 0.5–1 mm. in diameter; peridium soon becoming finely fimbriate to base and somewhat twisted or incurved; peridial cells usually seen only in side view, rhomboid, very thick, 30–35 x 60–90 μ , outer wall medium thin, 2–3 μ , smooth, inner wall medium thick, 7–10 μ , rugose, side walls very coarsely rugose with thick, somewhat irregular ridges, roundish or elongate ridge-like papillæ interspersed; æciospores globoid, very large, 28–35 x 30–45 μ , wall chestnut-brown, thick, 3–5 μ , rather finely verrucose.

III. *Telia* caulicolous, appearing on hemispheric swellings (1–4 cm. long) breaking forth along the sides of the larger branches or on subglobose galls (1.5–2 cm. in diameter) on the smaller branches, appanate, indefinite, usually of considerable size, often covering the whole hypertrophied area, sometimes becoming patelliform when expanded, chocolate-brown; teliospores 2-celled, ellipsoid, 18–28 x 42–61 μ , usually slightly narrowed both above and below, slightly or not constricted at the septum, wall cinnamon-brown, 1–1.5 μ thick; pores usually 3 in upper cell, 1 apical, 2 near the septum, in the lower cell 2 pores near the septum.

O and I on apple and mountain ash.

III. *Telia* on *Juniperus communis* and *J. sibirica*.

The teliospores occur on both twigs and leaves. Marked deformation is caused by this stage on leaves and petioles.

G. clavipes C. & P. (= *G. germinale* [Schw.] Kern)

I. *Æcia* (= *Ræstelia aurantiaca*) on stems and fruits, crowded on hypertrophied areas of various size on the twigs and peduncles, occupying part or nearly all of the surface of the fruits, cylindric, 1.5–3 mm. high by 0.3–0.5 mm. in diameter; peridium whitish, becoming coarsely lacerate, sometimes to base, erect or spreading; peridial cells seen in both face and side views, polygonal-ovate or polygonal-oblong in face view, 19–39 x 45–95 μ , rhomboid in side view, 25–40 μ thick, outer wall moderately thick, 3–5 μ , inner wall very thick, 13–23 μ , coarsely verrucose with loosely set, large, irregularly branched papillæ, side walls verrucose on inner half, similar to inner wall; æciospores globoid, large, 31–32 x 24–39 μ , wall pale yellow, thick, 3–4.5 μ , rather coarsely verrucose with crowded, slightly irregular papillæ.

III. *Telia* caulicolous, appearing on slight fusiform swellings, usually aggregated, roundish, 1–4 mm. across, often confluent, hemispheric, 1–3 mm. high, orange-brown; teliospores 2-celled, ellipsoid, 18–26 x 35–51 μ , roundish or somewhat acutish above, obtuse below, slightly or not constricted at the septum, wall yellowish, 1–2 μ thick, slightly thicker at the apex; pedicles carotiform, 9–19 μ in diameter near the spore; pores one in each cell, apical in the upper, near the pedicel in the lower.

I. *Æcia* on *Amelanchier*, *Aronia*, hawthorn, quince, and apple.

III. *Telia* on *Juniperus communis* and *J. sibirica*.

G. nidus-avis Thaxt.

I. *Æcia* amphigenous, especially fructicolous, cylindric, 2–4 mm.

high by 0.4–6.7 mm. in diameter; peridium soon becoming irregularly lacerate, usually to base, slightly spreading; peridial cells seen in both face and side views, lanceolate in face view, 15–23 x 55–88 μ , linear in side view, 14–18 μ thick, outer wall, 1.5 μ thick, smooth, inner and side walls 5–7 μ thick, coarsely rugose with narrow ridges, with shorter, often roundish papillæ interspersed; æciospores globoid or broadly ellipsoid, 18–23 x 23–28 μ , wall cinnamon-brown, rather thick, 2.5–4 μ , very finely verrucose, appearing almost smooth when wet.

III. *Telia* caulicolous, often dwarfing the young shoots and causing bird's nest distortions or witches' brooms, usually causing a reversion of the leaves to the juvenile form, sometimes appearing on isolated areas on the larger branches and producing gradual enlargements, solitary or rarely confluent, of variable size and shape, roundish to oval on the young shoots, 1–2 mm. across, oval to nearly elliptic on the woody branches, 1.5–3 mm. wide by 2–7 mm. long, pulvinate when young, becoming hemispheric, dark reddish-brown; teliospores 2-celled, ellipsoid, 16–23 x 39–55 μ , wall pale cinnamon-brown, rather thin, 1–1.5 μ , very slightly thicker at apex; pores one in a cell, apical. Mycelium perennial in leaves, branches or trunks of *Juniperus virginiana*, very commonly inducing a "bird's nest" distortion.

I. *Æcia* on *Amelanchier* and quince.

III. *Telia* on *Juniperus virginiana*.

G. blasdaleanum (D. & H.) Kern occurs on the pear, apple and quince.

Uromyces Unger (p. 255)

Ö. Pycnia spherical with minute ostioles.

I. *Æcia* with peridia, spores without pores.

II. Urediniospores generally with many germ pores, unicellular, spherical, ellipsoid or variously shaped, usually rough.

III. Teliospores unicellular, pedicellate, with an apical germ pore.

The unicellular teliospores may be distinguished from unrediniospores by their single apical germ pore, also usually by their thicker walls and absence of the roughness so characteristic of urediniospores.

The genus is a very large one with hundreds of species which exhibit heterœcism, autœcism, biologic specialization and the various types regarding spore forms that are noted on pages 231–235.

U. appendiculatus (Pers.) Fries

I. Aeciospores angularly globose, whitish, slightly punctulate, $17-32 \times 14-20 \mu$. II. Urediniospores pale-brown, aculeolate, $24-33 \times 16-20 \mu$. III. Teliospores elliptical or subglobose, smooth, dark-brown, apex much thickened, with a small, hyaline, wart-like papilla, $26-35 \times 20-26 \mu$.

An autœcious eu-type. On Phaseolus, Dolichos and other related legumes.

The sori usually appear late in the season on leaves, rarely on stems and pods. The mycelium is local. Great difference in varietal susceptibility is noted. The existence of two biologic forms has been demonstrated.



FIG. 257.—Diagrammatic section of uredinium of *U. appendiculatus*. After Whetzel.

lacerate, somewhat revolute; spores broadly ellipsoid, $18-26 \times 15-21 \mu$, with thin, colorless, finely verrucose walls.



FIG. 258.—Diagrammatic section of teliospores of *U. appendiculatus*. After Whetzel.



FIG. 259.—*Uromyces appendiculatus*, teliospore germinating. After Tulasne.

II. Uredinia amphigenous, scattered, roundish, cinnamon-brown; spores broadly-ellipsoid, $22-30 \times 17-25 \mu$; wall light golden-brown, sparsely echinulate.

III. Telia roundish or elongate, soon naked, blackish-brown; spores ellipsoid or ovoid, $25-39 \times 18-25 \mu$, wall dark chestnut-brown, $1.5-2.5 \mu$, thickened at apex, $6-10 \mu$, smooth; pedicels once to twice length of spore, firm, persistent.

An autœcious eu-type common on many species of *Lathyrus* and *Vicia*.

U. trifolii (Hedw.) Lév. An autœcious eu-type.

I. *Æcia* in circular clusters, on pallid spots. Peridia shortly cylindric, flattish, on the stems in elongated groups; edges whitish, torn. Spores subglobose or irregular, finely verrucose, pale-orange, $14-23 \mu$ in diameter.

II. Uredinia pale-brown, rounded, scattered, surrounded by the torn epidermis. Spores round or ovate, with three or four equatorial germ pores, echinulate, brown, $20-26 \times 18-20 \mu$.

III. Telia small, rounded, almost black, long covered by the epidermis. Spores globose, elliptical or subpyriform, with wart-like incrassations on their summits, smooth, dark-brown, $22-30 \times 15-20 \mu$. Pedicels long, deciduous.

Cosmopolitan on white, crimson and alsike clovers. Stages O and I are most common on *Trifolium repens*, least common on *T. incarnatum*. Pycnia appear in early spring or even in winter. The *æciospores* germinate readily in water and on suitable hosts may give infections which give rise to urediniospores in about two weeks. Urediniospores may be produced throughout the summer and may even survive the winter. Teliospores are produced in the uredinia or in separate sori late in the season. The teliospores by infection give rise to the pycnial and *æcial* stages. Considerable distortion arises in parts affected by either stage.

U. fallens (Desm.) Kern. A form on crimson, zig-zag and red clover often confused with the last species.

O and I unknown.

II. Urediniospores with four to six scattered germ pores.

III. Teliospores similar to those of *U. trifolii*.

U. medicaginis Pass.

II. Uredinia chestnut-brown, spores globose to elliptic, $17-23 \mu$, light-brown.



FIG. 260.—Urediniospore and teliospore of *Uromyces trifolii*. After Cobb.

III. Telia dark-brown, spores ovate-elliptic or pyriform, 18–28 x 14–20 μ .

Pyenia and æcia unknown.

II and III on alfalfa.

U. caryophyllinus (Schr.) Wint.

II. Uredinia sparse, confluent on stems, spores round, elliptic or oblong, 40 x 17–28 μ , light-brown.

III. Teliospores globose, irregular or ovoid, apex thickened, 23–35 x 15–22 μ , pedicel 4–10 μ .

II and III on cultivated carnations and several other members of the genus *Dianthus*. I on *Euphorbia gerardiana*. It has been known in Europe since 1789 but was not noted in the United States until 1890. It is now widespread.

U. betæ (Pers.) Tul. An autœcious eu-type; on members of the genus *Beta* both wild and cultivated.

U. oblongus Vize is an autœcious opsis-type, I and III on various species of *Trifolium* throughout the Rocky Mountains and along the Pacific coast.

Puccinia Persoon (p. 255)

O, I, II, as in *Uromyces*.

III. Teliospores separate, pedicellate, produced in flat sori, consisting of two superimposed cells each of which is provided with a germ pore. The superior cell has its germ pore, as a rule, piercing its apex; in the inferior or lower the germ pore is placed immediately below the septum.

Mesospores (p. 234) are not rare. They are merely teliospores with the lower cell wanting, and function as teliospores.

Some one thousand two hundred twenty-six species are enumerated by Sydow, presenting great diversity in spore relation, heterœcism and biologic variation.

P. ribis-caricis Kleb.

I on *Ribes*. II and III on *Carex*.

Klebahn differentiates five species of *Puccinia* on *Ribes* belonging to the *Ribis-Carex* group, some of which, in particular *P. pringsheimiana*, do damage on the gooseberry.

P. asparagi DC.

I. Peridia in elongated patches upon the stems and larger branches, short, edges erect, toothed. Spores orange-yellow, round, very finely echinulate, 15–16 μ in diameter.

II. Uredinia brown, flat, small, long covered by the epidermis. Spores irregularly round or oval, clear-brown, echinulate. $18-25 \times 20-30 \mu$.

III. Telia black-brown, compact, pulvinate, elongate or rounded, scattered. Spores oblong or clavate, base rounded, apex thickened, darker, central constriction slight or absent, deep chestnut-brown, $35-50 \times 15-25 \mu$. Pedicels persistent, colorless or brownish, as long or longer than the spores.

An autœcious eu-type on asparagus, cultivated and wild. The fungus has been known in Europe since 1805 but did not attract attention in the United States until 1896.

The æcial stage appears in early spring; the æciospores may germinate at once or if dry remain viable for several weeks, their germ tubes penetrating the host in most cases stomatally. The uredinia appear in early summer soon after or with the æcial stage and, wind borne, distribute the fungus. The



FIG. 261.—Section through black rust pustule, showing teliospores of *P. asparagi*. After Smith.

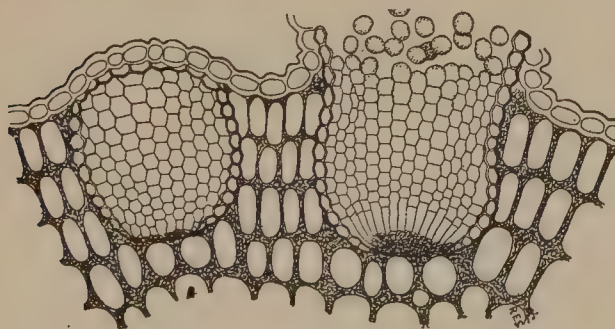


FIG. 262.—Cross section of æcia of *P. asparagi*. After Smith.

I (= *Æ. rubellum*). Æcia on circular red spots 0.5–1.5 cm. in diameter, shallow, edges white, torn. Spores white, subglobose, echinulate, $15-16 \mu$ in diameter.

II. Uredinia rather large, dark brown, elliptical, pulverulent, without paraphyses. Spores ovate or elliptical, echinulate, brown, $25-35 \times 15-23 \mu$.

III. Telia large, long, sooty black, thick, often confluent.

urediniospores remain viable a few months when dry. The telial stage appears late in the season and germinates only after hibernation.

Unicellular spores, mesospores, are sometimes met.

P. phragmitis
(Schum.) Koern.

Spores elliptical, rounded at both ends, markedly constricted in the middle, dark blackish-brown, smooth, $45-65 \times 16-25 \mu$. Pedicels very long, $150-200 \times 5-8 \mu$, yellowish, firmly attached.

Heterœcious; I on *Rumex* and rhubarb, II and III on *Phragmites*.

P. fraxinata (Lk.) Arth. causes rust of ash.

P. subnitens Diet. occurs in æcial form on the sugar beet and spinach as well as on various genera of twenty-two families of dicotyledonous plants. The uredinial and telial stages are on the grass *Distichlis*. There are but one or two rusts in the world that can compare with this in host range.

P. hieracii (Schum.) H. Mart. is a brachy-puccinia, common on chicory, endive, dandelion and a number of related hosts.

P. arachidis Speg., known only in its uredinial and telial stages, is a serious parasite of peanuts.

P. graminis Pers.

O. Pycnia amphigenous, numerous, honey-yellow becoming brownish, globoid, $90-110 \mu$ in diameter; ostiolar filaments $30-60 \mu$ long.

I. (= *Æ. berberidis*). Spots generally circular, thick, swollen, reddish above, yellow below; peridia cupulate or cylindrical, with



FIG. 263.—*P. graminis*, telium and germinating teliospore.
After Carleton.

whitish, torn edges; spores angularly globoid or oblong, $15-19 \times 16-23 \mu$; walls appearing smooth when wet, finely and closely verrucose, colorless, thin, considerably thickened on one side; cell contents orange-yellow in fresh spores.

II. Uredinia reddish-brown, oblong-linear, often confluent,

forming very long lines on the stems and sheaths, pulverulent. Spores elliptical, ovate or pyriform, 21–42 x 13–24 μ , wall golden-brown with four very marked, nearly equatorial germ pores, echinulate, 1.5 to 2 μ thick.

III. Telia persistent, naked, linear, generally forming lines on the sheaths and stems, often confluent; spores fusiform or clavate, 35–58 x 16–23 μ , constricted at the septum, generally attenuated below, apex much thickened, 5–10 μ , rounded or pointed, wall smooth, chestnut-brown above, paler below, 1–1.5 μ thick; pedicels long, persistent, golden brown near spore and paler at base.

O and I on *Berberis* and *Mahonia*.

II and III on *Avena*, *Hordeum*, *Secale*, *Triticum* and nearly 100 other grasses.¹ Of great importance on wheat.

This fungus was the subject of the classic researches of de Bary begun in 1865 and has since repeatedly served as the basis of fundamental investigations in parasitism, cytology and biologic specialization. That the barberry æciospores can bring about cereal infection seems to have been shown as early as 1816. Inoculations in the reverse order were made in 1865. What was formerly regarded as one species, *P. graminis*, must now be separated on biologic grounds into many races; more than 30 have been recognized on *Triticum*, each of which is limited in its parasitism to certain varieties and species of host. The chief races are: *P. graminis secalis*, *P. graminis avenæ*, *P. graminis tritici*, *P. graminis airæ*, *P. graminis poæ*, *P. graminis phlei-pratensis*, *P. graminis agrostis*, *P. graminis tritici-compacti*.

The work of Stakman and others in this country has added much to our knowledge of biologic specialization in this rust. It has been shown that biologic forms are restricted to certain hosts so that, contrary to earlier beliefs, no "bridging hosts" capable of extending the parasitism to grasses ordinarily immune, have been found. Thus *P. graminis tritici*, which, in the light of very recent work, may represent a number of forms, attacks wheat and barley readily, rye slightly, and oats not at all; *P. graminis secalis* attacks rye and barley readily, oats weakly, and wheat is free from attack; likewise *P. graminis avenæ* attacks oats readily, rye, and barley weakly, while wheat is immune. It appears that certain biologic forms have one or more hosts, e. g., barley, in common, and it was the lack of proper recognition of this which caused earlier

¹ Arthur, J. C. N. Am. Flora 7: 295, 1920.

investigators to assume that one biologic form could be changed into another by passage through certain hosts.

While these forms have many morphological features in common, differences have been found in the urediniospores which are more or less characteristic of the different forms.¹ The following table shows the difference in size of spores.

Comparative sizes of urediniospores of biologic forms of *Puccinia graminis*

<i>Biologic form</i>	<i>Size Limits, μ</i>	<i>Mode Averages, μ</i>
<i>P. graminis tritici</i>	23.04–41.92 x 15.04–24.96	32.36 x 19.82
<i>P. graminis tritici-compacti</i>	23.68–40.00 x 14.40–25.28	31.72 x 19.48
<i>P. graminis secalis</i>	17.92–38.72 x 13.44–21.44	27.14 x 17.26
<i>P. graminis avenæ</i>	19.20–37.12 x 13.76–25.60	28.48 x 19.46
<i>P. graminis phlei-pratensis</i> .	16.00–32.00 x 11.84–21.12	23.04 x 17.24
<i>P. graminis agrostis</i>	15.04–31.68 x 12.16–20.48	22.48 x 15.95

The mycelium branches intercellularly and bears small haustoria which penetrate the cells. In the barberry it is local. The epiphyllous pycnia appear first, followed soon by the mainly hypophyllous æcia. The flask-shaped pycnia at maturity bear numerous pycniospores and exserted paraphyses. Their hyphæ are orange-tinted, due to a coloring matter in the protoplasm or later in the cell walls.

The æcium originates in the lower region of the mesophyll from a hyphal weft. The fertile branches give rise to chains of spores every alternate cell of which atrophies. The outer row of sporophores and potential spores remains sterile to form the peridium. When young the æcium is immersed and globular, at maturity erupts and forms an open cup. These spores germinate by a tube capable upon proper hosts of stomatal infection and following this of producing the uredinium.

Urediniospores are produced throughout the season even through the winter on autumn sown grain under the proper conditions in the South.

They remain viable for weeks and doubtless serve hibernation purposes at least in the warmer sections of this country. In colder

¹Stakman, E. C. and Levine, M. N. Effect of certain ecological factors in the morphology of the urediniospores of *Puccinia graminis*. Jour. Agr. Res. **16**: 43, 1919.

sections they occasionally live over in more or less sheltered spots in the field.

Teliospores arise later in the season in the uredinia or in separate telia. Unicellular teliospores, mesospores, are occasionally seen. Teliospores germinate best after normal outdoor hibernation, producing the typical 4-celled promycelium, long sterigmata and solitary basidiospores. If under water the usual promycelium becomes abnormal and resembles a germ tube.

Basidiospores were shown by de Bary, confirmed by Ward and Eriksson, to be incapable of infecting wheat leaves. Jaczewski succeeded in securing germination of pycniospores but the resulting mycelium soon died and infection was not attained.

***P. dispersa* Erik.**

I (= *Æ. asperifolium*, Pers.). Spots large, generally circular, discolored, generally crowded. Peridia flat, broad, with torn, white edges; spores subglobose, verrucose, orange-yellow, 20–25 μ .

II. Uredinia oblong or linear, scattered, yellow, pulverulent. Spores mostly globoid or ovate, echinulate, with six germ pores, yellow, 20–30 x 17–24 μ , wall golden yellow.

III. Telia small, oval or linear, black, covered by epidermis, surrounded by a brownish stroma; spores oblong or elongate, cuneiform, slightly constricted, the lower cell generally attenuated, apex thickened, truncate or often obliquely conical; spores smooth, brown, variable in size, 40–60 x 15–20 μ ; pedicels short.

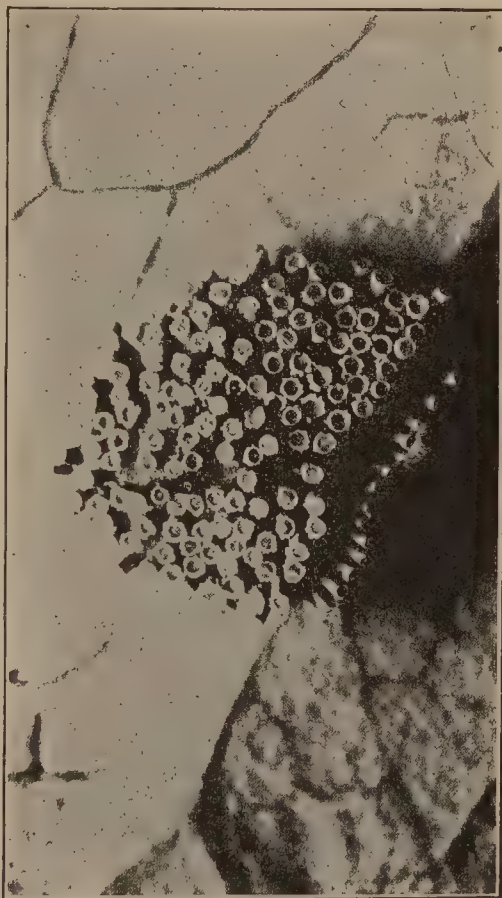


FIG. 264.—A portion of a barberry leaf, greatly enlarged, showing cluster cups which contain the spores. After U. S. Dept. Agr.

Heterœcious; O and I on Boraginaceæ.

II and III on rye. The teliospores germinate as soon as mature.

P. triticina Erik. on wheat is the most common and widely distributed of all rusts of the United States. Ordinarily only the uredinial stage is seen, due to the telia being minute and covered.



FIG. 265.—*P. dispersa*, section of uredinium. After Bolley.

It has been demonstrated that several species of *Thalictrum* may bear the æcia.¹ The teliospores germinate in the spring after a resting period.

Bolley has shown it capable of hibernation by urediniospores and by live winter mycelium and it has further been shown that the spores themselves can survive freezing in ice. The æcial stage can be entirely omitted.

On morphological characters this rust cannot be distinguished from that found on a large number of wild grasses, including species of *Agropyron*, *Bromus*, *Elymus* and *Poa*. Arthur has accordingly combined these forms under one species, recognizing in it a number of biologic races.²

P. coronata Cda.

I (= *Æ. rhamni*). Æcia often on very large orange swellings, causing great distortions on the leaves and peduncles, cylindrical, with whitish, torn edges. Spores subglobose, 15–25 x 12–18 μ , wall thin, colorless, very finely verrucose, orange-yellow.

¹ Jackson, H. S. and Mains, E. B. Æcial stage of the orange leaf rust of wheat, *Puccinia triticina* Eriks. Jour. Agr. Res. **22**: 151, 1921.

² Arthur, J. C. N. Am. Flora **7**: 333, 1920.

II. Uredinia orange, pulverulent, elongated or linear, often confluent. Spores globose or ovate, $20-28 \times 15-20 \mu$, wall thin, pale yellow with 6-8 scattered germ pores, finely echinulate, orange-yellow.

III. Telia persistent, black, linear, often confluent, long covered by the epidermis. Spores subcylindrical or cuneiform, attenuated below, constriction slight or absent, apex truncate, somewhat



FIG. 266.—*P. coronata*, various teliospore forms. After Bolley.

thickened, with six or seven curved, blunt processes, brown, $40-60 \times 12-20 \mu$. Pedicels short, thick.

Heteroecious; O and I, on *Rhamnus*, *Lepargyrea*, *Berchemia* and *Eleagnus*.

II and III on about 40 grasses including oats and timothy.

Infection experiments have shown that a number of different races, inseparable on a morphological basis, exist.

P. glumarum (Schmidt) Erik. & Henn. is widely distributed on wheat, rye, barley and a number of other grasses. It was first recognized in the United States in 1915. While its effect on the host is quite different from that of *P. triticina* and *P. dispersa*, producing elongated streaks, with the sori linearly disposed, the urediniospores and teliospores of this rust are very similar to those of the two rusts mentioned. In fresh material there is a difference in the color of the uredinial material so that it is commonly called yellow leaf rust, while the others are known as orange leaf rusts.

No aëcial host has been found.

P. simplex (Koern.) Erik. & Henn.

O and I on *Ornithogalum umbellatum*.

II and III on barley.

P. sorghi Schw.

I (= *Æ. oxalidis*). Aëcia hypophyllous, in small circular groups, 2-3 mm. broad, cupulate, 0.2-0.3 mm. in diameter; peridium fragile, margin erect, irregularly lacerate or entire; peridial cells

oblong, $15-18 \times 23-32 \mu$; æciospores globoid or ellipsoid, $13-19 \times 18-26 \mu$.

II. Uredinia amphigenous, scattered or in groups; spores globose to ovate, $23-30 \times 22-26 \mu$, very finely echinulate.

III. Telia amphigenous, black. Spores ovate-oblong or clavate-obtuse, constricted, $28-45 \times 12-17 \mu$, spore wall chestnut-brown,



FIG. 267.—*Puccinia sorghi*. After Scribner.

$1-2 \mu$ thick, moderately thickened above, $5-7 \mu$; pedicel once to twice length of spore, persistent.

Heteroecious. O and I on *Oxalis*. II and III on *Zea*. Of little economic importance.

The relation of the æcial stage was demonstrated by Arthur; it is believed, however, that hibernation is largely by the urediniospores.

P. purpurea Cke. Amphigenous, spot purplish, sori irregular, dark-brown.

II. Urediniospores ellipsoid or oblong, $29-40 \times 23-31 \mu$, wall thick, $1.5-2 \mu$, cinnamon-brown, finely and closely verrucose, echinulate.

III. Teliospores elongate, ovate, brown, long-pedicellate, $40-45 \times 22-25 \mu$. On *Sorghum*.

P. poarum Niels. occurs on bluegrass and other grasses.

P. malvacearum Bert.

III. Telia yellowish-brown at first, later darker, compact, round, pulvinate, elongate on the stems, scattered, seldom confluent, pale reddish-brown. Spores fusiform, attenuated at both extremities, apex sometimes rounded, constriction slight or absent, apical thickening, slight, smooth, yellow-brown, $35-75 \times 15-25 \mu$. Pedicels firm, long, sometimes measuring 120μ .

A lepto-puccinia on various species of *Althea*, *Malva*, etc.; particularly serious on the hollyhock. A native of Chili, it was first known as a pest in Australia; soon afterward in Europe. It seems to have entered the United States sometime prior to 1886 and is now almost universal. The teliospores germinate immediately in suitable environment, mainly from the apical cell, or may



FIG. 268.—*P. malvaccarum*. After Holway.

remain alive over winter and originate the spring infection. The mycelium also hibernates in young leaves. Mesospores are common. 3 to 4-celled teliospores are also met.

***P. chrysanthemi* Roze.**

II. Uredinia chocolate-brown, single or in circular groups, hypophyllous, rarely epiphyllous. Spores spherical to pyriform. Membrane spiny and with three germ pores, $17-27 \times 24-32 \mu$.

III. Telia dark-brown, hypophyllous. Teliospores rarely in uredinia, dark, obtuse, apex thickened, membrane thick, finely spiny, $20-25 \times 35-43 \mu$. Pedicel $1-1\frac{1}{2}$ times the spore length.

On cultivated *Chrysanthemum*. In many places urediniospores

may be produced continuously and teliospores be but rarely seen, thus in America only urediniospores have been found. It was first seen in America in 1896 and soon spread over the country. Numerous inoculation trials go to show that it is independent of the other rusts common on nearly related Compositæ.



FIG. 269.—*P. helianthi*, uredinio- and teliospores. After Cobb.

***P. helianthi* Schw.**

O. Pycnia clustered.

I. *Æcia* in orbicular spots; peridial margins pale, torn; spore wall colorless.

II. Uredinia minute, round, chestnut-brown, spores globose to ovate, 23–34 x 19–26 μ , minutely spiny.

III. Telia round, dark-brown to black; spores rounded at base, slightly constricted, 38–50 x 20–27 μ , smooth; pedicel hyaline, equal to or longer than the spores.

Autœcious on numerous species of *Helianthus*, consisting of numerous biologic forms. Imported from America to Europe.

Other less important species are on umbellifers, onion, endive, *Centaurea*, dandelion, chicory, buckwheat, mints, bluegrass, *Dianthus*, violet, canna, *Antirrhinum*, *Vinca*.

Uredinales Imperfecti ¹ (p. 241)

KEY TO Uredinales Imperfecti

Spores catenulate

Peridium absent 1. *Cæoma*, p. 279.

Peridium present

Toothed, body cup-shaped 2. *Æcidium*, p. 278.

Fimbriate, body elongate 3. *Ræstelia*, p. 280.

Irregularly split 4. *Peridermium*, p. 279.

Spores not catenulate 5. *Uredo*, p. 280.

Æcidium Persoon

Spores surrounded by a cup-shaped peridium; produced catenulate in basipetal series. Germination as in *Uredo*.

The species are very numerous and belong in the main to *Puc-*

¹ Johnson, A. G. The unattached æcial forms of plant rusts in North America. Proc. Ind. Acad. Sc. 1911, 375.

cinia and Uromyces. Most of the forms of economic interest are found under these genera. A few others of occasional economic bearing whose telial stage has not yet been recognized are given below.

Æ. brassicæ Mont. on Brassica is perhaps identical with *Puccinia isiacæ*. *Æ. gossypii* occurs on cotton.

Cæoma Link (p. 278)

Sori without a peridium, accompanied by pycnia, with or without paraphyses, produced in chains; germination as in *Uredo*.

The forms are mostly stages of *Melampsora*, *Phragmidium* or their kin. Those of economic interest are found under *Gymnoconia* and *Melampsora*.

Peridermium Léviellé (p. 278)

Pycnia truncate-conic.

Peridia caulicolous or foliicolous, erumpent, saccate to tubular, lacerate-dehiscient, spores catenulate or at maturity appearing solitary, globose to elliptic or oblong, polyhedral by pressure, yellowish-brown; peridial cells with inner walls roughened.

The æcial stages of *Coleosporium*, *Cronartium*, *Pucciniastrum*, *Melampsorella* and *Chrysomyxa*.

The peridia usually extend conspicuously above the host surface and rupture irregularly by weathering.

All of the species grow on the Coniferæ, most of them on *Pinus*¹ on leaves, branches and bark. On the leaves the æcia are much of the type shown in Fig. 247. When on the woody part great distortion may be caused by the perennial fungus and much injury result to the wood.

The mycelium may live intercellularly in rind, bast and wood of pine and continues to extend for years causing swellings. Pycnia are either subcuticular or subepidermal and the pycniospores often issue in a sweetish liquid. Æcia occur as wrinkled sacs emerging from the bark of the swollen places and bear spores perennially.

A key to some thirty species is given by Arthur & Kern. So far as it relates to the distribution of the *Peridermiums* to their telial genera it is as follows:

¹ Arthur, J. C. and Kern, F. D. North American species of *Peridermium* on pine. *Mycol.* **6**; 109, 1914.

KEY TO ASSIGNMENT OF SPECIES OF *Peridermium**Pycnia subcuticular*

- Æcia* cylindrical..... **Pucciniastrum.**
Æcia tongue-shaped..... **Melampsorella, Melamp-soridium.**

Pycnia subepidermal

- Æcial* peridia one cell thick
 On *Pinus*..... **Coleosporium.**
 On *Picea*..... **Melampsoropsis.**
 On *Abies*..... **Uredinopsis.**

Pycnia subcorticular

- Æcial* peridia more than one cell thick... **Cronartium.**

Such forms as are of economic interest and of which the telial stage is known are discussed under *Coleosporium*, *Cronartium*, *Melampsorella*, and *Pucciniastrum*.

Several other forms are found on pine, spruce and *Tsuga*.

Roestelia Rebentisch (p. 278).

FIG. 270.—*R. pyrata*, cups showing peridial cells.
 After King.

O. *Pycnia* spherical or cup-formed.

I. *Æcia* with strongly developed, thick-walled peridia, flask-shaped or cylindrical; spores globose, 1-celled,

brown to yellow, catenulate, with several evident germ pores.

The forms are the *æcial* stages of *Gymnosporangium* and occur on rosaceous hosts. The economic forms will be found under *Gymnosporangium*.

Uredo Persoon (p. 278)

Spores produced singly on the terminal ends of mycelial hyphæ; germination by a germ-tube which does not produce basidio-spores, but enters the host-plant through the stomata.

These forms are in the main discussed under their telial genera.

Eubasidii (p. 211)

The *Eubasidii* represent the higher development of the basidia-fungi and contain the majority of the species. The basidia, the typical club-shaped undivided stalks, bear usually four, sometimes two, six, or eight unicellular spores on a like number of sterigmata and are mostly arranged in **hymenia**. There is great diversity in

the form and size of the sporophore from an almost unorganized mycelial microscopic web to the large complex structures of the toad stools and puff balls. Conidia and chlamydospores while occasionally present are much less common than in the preceding groups or orders.

The cells of the sporophore in many forms investigated are binucleate, Fig. 272, in other forms they are multinucleate.

The origin of the binucleate condition often antedates the formation of the sporophore and may occur far back in the mycelium,

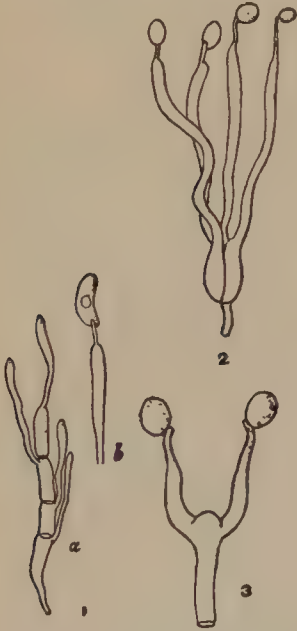


FIG. 271.—Various basidia of the lower basidiomycetes, 1, auricularias; 2, tremellas with longitudinal divisions; 3, dacryomycetes with undivided forked basidium.



FIG. 272.—Hypochnus, semi-diagrammatic section showing development of hymenium and basidia, with nuclear conditions. After Harper.



FIG. 273.—Mycelium of Hypochnus showing clamp connections. After Harper.

perhaps as far back as the germinating basidiospore itself. In the basidial layer, however, even of those forms with multinucleate vegetative cells, the nuclei are reduced to two so that the general statement is permissible that in the hymenial layer of the Basidiomycetes the cells are binucleate. From such cells two nuclei wander into the basidium primordium where they fuse to one, reducing this cell to a uninucleate condition. This nucleus by two mitoses gives rise to four nuclei which wander through the sterigmata into the spores and constitute the four basidiospore nuclei.

The significance of this phenomenon of fusion in the basidium followed by division, which is widespread and apparently the dominant typical phenomenon among the Basidiomycetes including both high forms, Agarics, and low forms, Dacryomycetes, the Uredinales and even the Gasteromycetes, is much debated. By some it is regarded as a very much modified type of fertilization, a view to which support is lent by the fact that in some of these fungi, perhaps all, the nuclei multiply by a process of conjugate division. Thus the two nuclei found in the young basidium, although belonging to the same cell may in ancestry be very distantly related.

Agaricales

Stroma usually well developed, fleshy, coriaceous, leathery or woody; spores arising from basidia which form a distinct membranous hymenium which is naked at maturity, and fre-



FIG. 274.—Stages in the development of the basidium (*Agaricus*): original binucleate condition followed (E-F) by fusion, and subsequent mitosis N-R, resulting in four spore nuclei. After Wager.

quently covers the surface of gills, pores or spines (Hymenomycetes).

This is a very large order of over eleven thousand species.

The mycelium grows to long distances over or through the supporting nutrient medium, often forming conspicuous long-lived resistant rhizomorphic strands or sheets, sometimes developing sclerotia or again appearing as a mere floccose weft.

The basidia bear four simple spores, in rare cases two, six or eight. Other forms of spores are found in some species and chlamydospores may be borne either externally on the sporophore, in the hymenium, or inside of the sporophore tissue. In the lowest forms the basidia arise directly from the mycelium without the formation of any definite sporophore but in most species the sporophore is highly complex, consisting of large, stalked or sessile, pseudoparenchymatous structures toad-stools, mushroom, etc., on special surfaces of which, the hymenium, Fig. 276, lies, covering gills or spines or lining pits or pores.

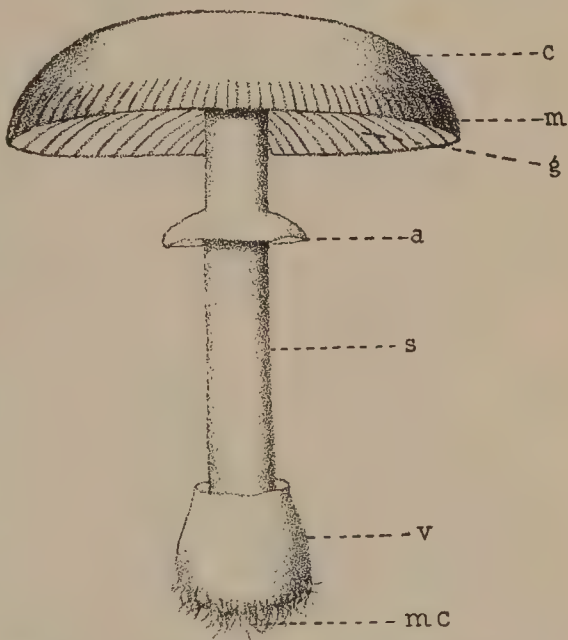


FIG. 275.—An agaric (*Amanita*) sporophore showing parts: c, pileus; m, striated margin; g, gills; a, annulus; s, stem; v, volva; mc, mycelium. After Peck.

The general relation of the basidia to the hymenium and the sporophore is shown in Fig. 276. Families are delimited by the character of the sporophore, distribution of the hymenial surfaces, presence of cystidia, size and color of spores, and other more minor points.

In germination the spore produces a germ tube which develops directly into a mycelium. In many species the young mycelium is conidia-bearing.

Cytologically the group conforms to the general description given on page 281.

The Agaricales are chiefly of interest to pathologists as wood fungi though in a comparatively few instances they are found on herbs. Upon wood they may do harm. First, as root parasites, in which case death may follow through interference with absorption or anchorage. Second, as causes of heart rots leading to weakness and eventual overthrow of the tree. Third, as parasites of sap wood, cambium or bark leading to death of a part of the host and often its complete loss.

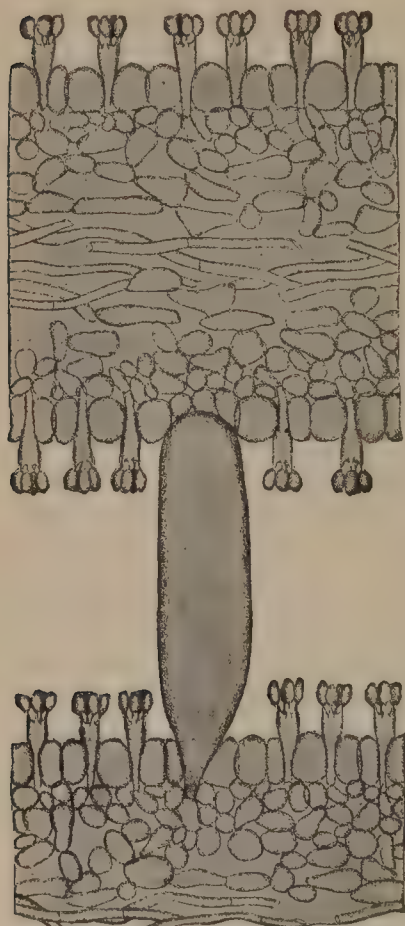


FIG. 276.—Cross section of the gill showing basidia, sterigmata and spores, also a cystidium stretching from one gill to the next. After Buller.

In many instances the fungus draws its subsistence from host cells not actually alive and hence strictly speaking they are saprophytes. Nevertheless, since their ultimate effect upon the tree is to cause disease or death, from the practical viewpoint these fungi are pathogenic. Many species, moreover, can start their career on a host plant as saprophytes and after attaining a stage of vigorous vegetative growth become truly parasitic. In most instances they are **wound parasites**, which cannot gain access to the inner portions of the host through uninjured tissue but must make entrance through some wound, as those due to hail, wind, snow, insects, man and other animals.

Within the tissues the mycelium may cause the disappearance of substances, e. g., *Fomes igniarius* consumes the tannin, or the mycelium may secrete enzymes which penetrate the host to long distances. These may dissolve first one component of the cell, e. g., the lignin, next the most lignified residue, the middle lamella, resulting in dissolution of the tissue. In other cases the parts of the cell walls other than the middle lamella are first affected and soon shrink, resulting in cracks. Fig. 279. Some fungi cause char-

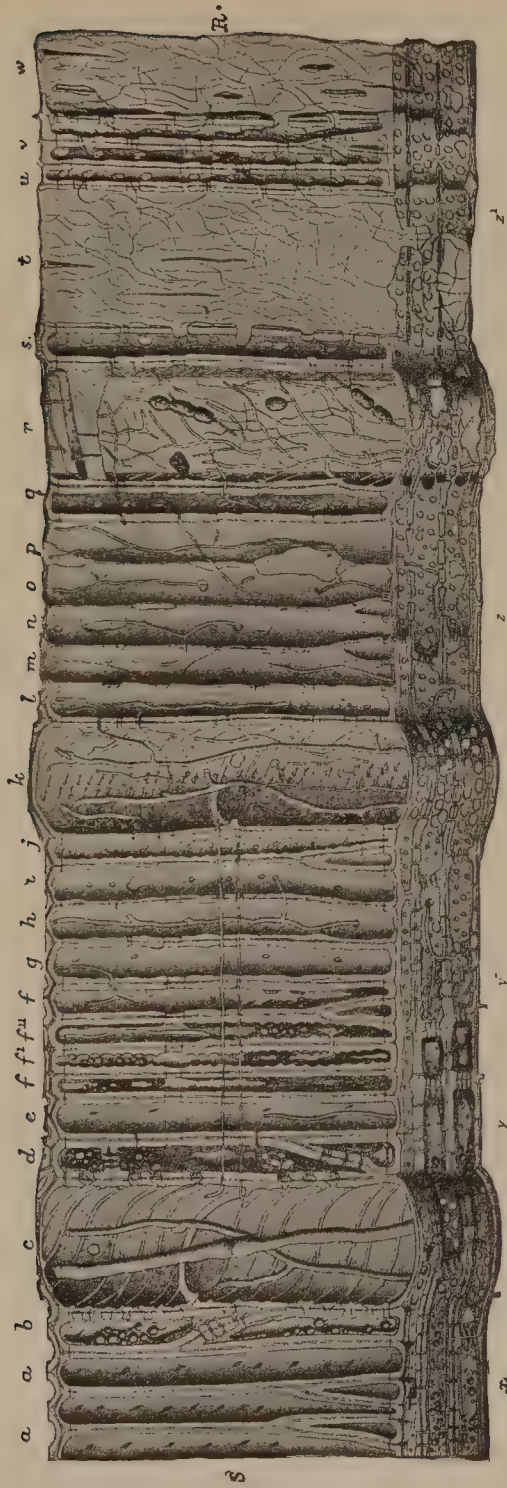


FIG. 277.—“Radial-longitudinal section; *u*, *v* and *f* are the autumn wood cells of two successive yearly rings. The mycelium has destroyed the less lignified fibres. In *h* and *i* the secondary thickening has begun to be acted upon. In *m*, *n*, *o* and *p* the secondary thickening has almost disappeared, and the middle lamellæ are in process of solution. In the region *t* the fibres have disappeared, leaving a space partly filled with hyphæ. The medullary ray cells *x* to *z*, the autumn wood cells *u*, *v*, and the vessel *r*, with its surrounding cells *q* and *s*, *i*, *e*., the highly lignified elements, are seen to be more persistent.

“The enlargement of the pits of the medullary ray cells may be traced from *x* to *z*.
“Holes made by hyphæ through cell-walls are shown in the vessel *k*, also in *f*, *h*, *l*, *n*, and *o*, upon radial walls, while the holes on the tangential walls in the cells *u* and *v* have been made in a similar manner.

“The browning and disappearance of the protoplasm, and the disappearance of starch grains can be traced in the medullary ray from *x* to *y*, and in the wood parenchyma and autumn wood cells from *b* to *q*.

“The largest hyphæ having clamped connections are to be seen in the freshly entered vessel *c*. In the vessel *k* the hyphæ are more numerous, the larger ones also with clamp-connections. In the most highly rotten wood, *q* and *w*, the hyphæ are much smaller.” After Buller.

acteristic color changes particularly in those cell walls which are rich in carbon. Parasitism in this group is ancient, since good examples of agarics growing on wood are found as early as the Tertiary period.

These fungi spread to new hosts by spores borne in various ways; by insects (*Trametes radiciperda*), animals, wind (*Polyporus pinicola*) etc., or in a purely vegetative manner by the mycelium which in the form of rhizomorphs (*Armillaria mellea*) travels through the ground to considerable distances.



FIG. 278.—Tracheid of pine decomposed by *Trametes pini*. The primary wall dissolved in the lower part, the secondary and tertiary layers are only of cellulose. The mycelium makes holes at places. After Hartig.



FIG. 279.—Pine tracheid acted upon by *Polyporus schweinitzii*. The cellulose had been extracted leaving the walls chiefly lignin. Drying has caused cracks. After Hartig.

The number of species of Agaricales which affect live plants in the ways mentioned above is large but in many instances research in this field has not yet revealed the true relation existing between the fungi and the woody plants upon which

they grow; whether they occur as parasites or as saprophytes; whether actually injurious or not. The species given below are mainly regarded as actually injurious. If more questionable cases were to be included the number would be increased several fold.

KEY TO FAMILIES OF Agaricales

- | | |
|---|-----------------------------------|
| Hymenium smooth, coriaceous or waxy,
rarely ribbed or papillate | |
| Sporocarp effused, resupinate or rarely
pileate, usually not fleshy | 1. <i>Thelephoraceæ</i> , p. 287. |
| Hymenium variously folded or pitted | |
| Hymenium with teeth, tubercles or
tooth-like plates which are sporo-
genous | 2. <i>Hydnaceæ</i> , p. 293. |
| Hymenium lining pores | |
| Pores not easily separating from the
pileus, which is commonly leath-
ery, corky or punky | 3. <i>Polyporaceæ</i> , p. 295. |
| Hymenium covering the surface of radi-
ating plates | 4. <i>Agaricaceæ</i> , p. 318. |

Thelephoraceæ¹ (p. 286)

Sporocarp coriaceous or waxy, resupinate or pileate, simple or compound; hymenophore smooth, rarely ribbed or papillate.

KEY TO GENERA OF **Euthelephoraceæ**

- Fructification consisting of only a fleshy hymenium on the surface of living leaves and shoots; basidia simple. 1. **Exobasidium**, p. 287.
- Fructification coriaceous or hard
 Basidia at first globose and simple, at length elongated and transversely septate, straight or curved, bearing sterigmata on the convex side; fructification resupinate. 2. **Septobasidium**, p. 292.
- Basidia simple, usually 4-spored
 Spores white or rarely bright colored, even or rarely uneven, neither setæ nor teeth present in the hymenium
 Fructification pileate ranging from infundibuliform and flabelliform to very narrowly reflexed forms; hymenium even. Some reflexed species may occur resupinate. 3. **Stereum**, p. 291.
- Fructification always resupinate, structure not cup-shaped; brown stellate organs not present in the subhymenial tissue; cystidia not present; structure compact or hypochnoid. 4. **Corticium**, p. 288.

Exobasidium Woronin

Strictly parasitic, the mycelium penetrating the host and usually causing marked hypertrophy and hyperplasia, producing leaf-galls and shoot-galls, bag-galls and bud-galls. The galls are composed principally of the tissues of the hosts with hyphæ between the cells. The form of the gall is dependent on: 1 the organ affected, 2 the degree of resistance, 3 the age of the organ. Hymenium unaccompanied by fleshy sporocarp, consisting only of the

¹ Burt. E. A. The Thelephoraceæ of North America. I. Ann. Mo. Bot. Gard. 1: 185, 1914.

closely-crowded, clavate basidia which break through the epidermis of the host.

The basidia bear two to four sterigmata and spores. The spores are mostly curved. Conidia are also found in some species. The

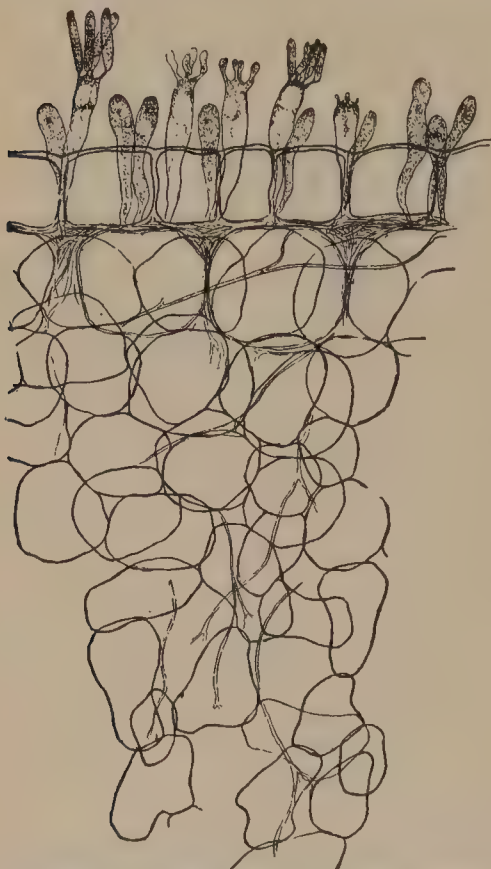


FIG. 280.—Exobasidium on Andromeda, showing host cells, mycelium, basidia and spores. After Richards.

basidiospores germinate with a germ tube which produces fine sterigmata and secondary spores capable of budding. The hymenial cells are binucleate, the two nuclei of the basidial cell fusing into one basidium-nucleus. This divides mitotically giving rise to the spore nuclei.

This genus among the basidia fungi is analogous to *Taphrina* among the ascus fungi.

Burt recognizes only three American, morphological species.

E. vaccinii (Fel.) Wor., with one variety, occurs on a wide range of ericaceous hosts including *Vaccinium*, *Andromeda*, *Rhododendron*, forming large blisters on the leaves, rarely on petioles and stems, discoloration red or purple. The fungus appears as a white

bloom on the under surface of the leaf; spores narrowly fusiform, $6-9 \times 1-1.5 \mu$. Basidia 2 or 4-spored.

Corticium Persoon (p. 287)

Hymenophore homogeneous in structure, membranous, leathery or fleshy, almost waxy, rarely approaching gelatinous; hymenium arising immediately from the mycelium, smooth or minutely warty; basidia clavate, simple with four to six sterigmata;

spores small, globose or ellipsoid, with a smooth colorless membrane.

C. koleroga (Cke.) v. Höhn=*Pellicularia koleroga* Cke.¹

Parasitic on branches and leaves of the coffee plant.

C. stevensii Burt.¹

Vegetative mycelium forms roundish or oblong, chestnut-brown sclerotia 3-4 mm. in diameter on the twigs; also slender mycelial strands, white when young, becoming chestnut-brown, along the twigs and petioles to the leaves and fructifying there. Fructifications at first downy and barely visible, soon thickening into a dirty pinkish-buff, felty membrane covering the whole under side of the leaf and frequently separable from it as a whole by mere

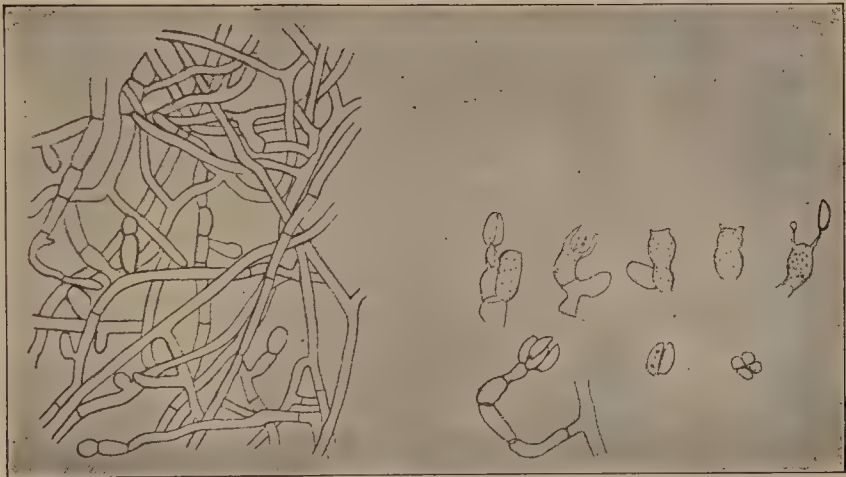


FIG. 281.—*C. stevensii*. Sporogenous reticulum prior to spore formation; basidia, sterigmata, and spores. After Stevens and Hall.

handling; hyphæ hyaline or slightly colored, giving their color to the fructifications, even, thin-walled, not incrusted, not nodose-septate, $4.5-7.5\ \mu$ in diameter; basidia scattered along the hyphæ on short lateral branches, simple, $11 \times 7-8\ \mu$, with four short sterigmata; spores hyaline, flattened or slightly concave on one side, $8-11 \times 3-4\ \mu$. Fructification 11 cm. long, 3-4 cm. broad, $45-60\ \mu$ thick, unbroken over whole under surface of leaves; sclerotia 3-4 mm. in diameter; mycelial strands 0.25-0.51 mm. in diameter, many centimeters long.

On apple, pear, *Viburnum*, and quince.

¹ Burt, E. A., *Corticiums causing Pellicularia disease of the coffee plant, hypochnose of pomaceous fruits, and Rhizoetonia disease.* Ann. Mo. Bot. Gard. 5: 119, 1918.

C. vagum B. & C.=*Hypochnus solani* Pr. & D.=*Rhizoctonia solani* Kühn.

Vegetative mycelium saprophytic in the soil and in wood in contact with the ground, and parasitic as the *Rhizoctonia solani*

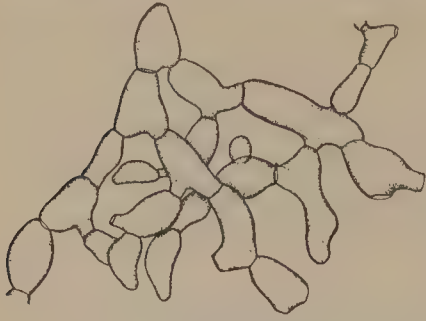


FIG. 282.—*C. vagum*. *Rhizoctonia* stage. After Duggar.

stage in underground, portions of various plants and forming at their surface underground, minute sclerotia; fructification a thin, arachnoid, perforate membrane more or less separable, pale olive-buff to cream color; 60–100 μ thick, composed of a few loosely interwoven hyphæ running along the substratum and sending out short branches which bear the basidia; hyphæ in contact with

substratum slightly brownish, hyaline elsewhere, not incrusted, not nodose-septate, up to 6–10 μ in diameter, with branches smaller; basidia not forming a compact hymenium, 10–20 x 7.5–11 μ , with 4–6 sterigmata 6–10 μ long; spores hyaline, flattened on one side, 8–14 x 4–6 μ . Fructification 5–15 cm. long on logs, 5–10 cm. broad, or in a collar 1–10 cm. long, sheathing the base of living stems.

The sterile mycelium (= *Rhizoctonia solani*) branches approximately at right angles and often forms sclerotia-like tufts with



FIG. 283.—*C. vagum*, from specimen on wood. *d*, hypha; *d1*, basidia, *d2*, spores. After Burt.

short, broad cells more or less triangular, which function as chlamydospores.

Brown to black sclerotial structures, a few millimeters in diameter, consisting of coarse, broad, short-celled hyphæ of peculiar

and characteristic branching also occur freely, both in nature and in culture, Fig. 282. Some of the various hosts upon which a *Rhizoctonia* apparently closely allied to that of *Corticium vagum* have thus far been found in America are:

Sugar-beet, bean, carrot, cabbage, cotton, lettuce, potato, radish, sweet potato, pumpkin, watermelon, garden pea, corn, purslane, *Solanum verbascifolium*, egg plant, pig-weed, spiny pig-weed, *Heterotheca subaxillaris*, *Richardia*, *Crotalaria*, *Cyperus rotundus*, *Heterotheca lamarekii* and *Phytolacca decandra*, *Pinus* sps., *Picea*, *Pseudotsuga*, carnation and alfalfa.

The sterile mycelium was noted in Europe on potato many years ago; its existence in America has been known since 1890. Its identity with the genus *Corticium* was demonstrated in 1904 by Rolfs by culture of the typical *Rhizoctonia* stage from the basidiospores.

The sterile mycelium occurs in two forms on the potato, a light-colored actively parasitic form usually somewhat deep in the affected tubers and a darker mycelium growing superficially on the host or over the soil. In artificial culture the manner of branching is typical, the young branches running nearly parallel to the main thread and bearing slight constrictions at their bases.

Corticium salmonicolor Berk & Br. = *Corticium lætum*, occurs on fig, apple, cacao, rubber, coffee, tea, grapefruit. In the Orient it is said to parasitize 141 species of plants. The cambium layer is the seat of the disease. The fungus spreads rapidly but is not a serious pathogen except in rainy periods in midsummer.

***Stereum* Persoon (p. 287)**

Hymenophore leathery or woody, persistent, of several layers, sometimes perennial, laterally or centrally attached; hymenium smooth.

The genus is chiefly wood inhabiting.

S. hirsutum (Willd.) Pers.

Hymenophore leathery, firm, expanded, wrinkled, hairy, yellowish; hymenium yellowish, smooth.

On hard woods and conifers.

S. frustulosum (Pers.) Fries, though sometimes found on living trees, is confined to dead wood. It causes a speckled rot of oak wood. Fig. 284.

S. purpureum Pers.

Hymenophore expanded, leathery, arched, grayish-white; hymenium smooth, purple.

This species is constantly associated with disease of drupaceous



FIG. 284.—Oak timber rotted by *Stereum frustulosum*. The lighter colored, irregular, small bodies are sporophores. After von Schrenk and Spaulding.

and pomaceous trees, manifest by a silvering of the leaves, death of branches and finally of the tree; also on apple, poplar, willow, birch and larch.

Septobasidium Patouillard (p. 287)

Fructifications resupinate, effused, coriaceous, producing probasidia upon the hyphæ at or near the hymenial surface; the probasidia remain attached to the hyphæ and either produce at the apex a few-celled, hyaline, spore-bearing filament, or elongate, become septate, and differentiate into such a filament, usually termed a transversely septate basidium; spores simple, hyaline, even, borne one to each cell by the terminal cell and next lower cells.

***S. pseudopedicellatum* Burt**

Fructification resupinate, effused, coriaceous, dry, not separable from the substratum, varying from avellaneous and wood-brown to cinnamon-brown, the margin undulate, withish; in structure three-layered, with (1) a layer next to the substratum of densely interwoven, thick-walled, slightly colored hyphæ $3\ \mu$ in diameter, which form (2) a layer of erect, hyphal pillars, or pedicels, each about $500\ \mu$ long, $20\text{--}40\ \mu$ in diameter, about 3–5 to a millimeter, whose hyphæ spread apart at the upper end of the pillars, branch and form and support (3) the hymenial crust about $300\ \mu$ thick, with hyphæ loosely interwoven near the pillars, $3\text{--}3.5\ \mu$ in diameter, very dense at the outer surface with the hyphal branches or paraphyses $2\ \mu$ in diameter, curved longitudinally along the surface and densely interwoven; erect probasidia nearly hyaline, rich in protoplasm, deeply staining, pyriform, $12\text{--}20 \times 8\text{--}15\ \mu$, are borne laterally on the hyphæ about $15\ \mu$ below the surface of the hymenium; spores white, simple, even, curved, $17\text{--}22 \times 4\text{--}5\ \mu$, borne singly from each of the upper three cells of a straight or flexuous, few-celled, hyaline organ which grows from the probasidium and protrudes above the surface of the hymenium.

On small, living branches of apple, orange, oak, dogwood, Nyssa, liquidambar; also on orange leaves. It attacks the bark, cambium and wood causing them to turn brown and die.

Hydnaceæ¹ (p. 286)

Sporophore variable in texture, cuticular, leathery, corky, felty, fleshy or woody; free and stipitate, shelving or resupinate; the hymenium warty, thorny, spiny or with tooth-like plates; basidia usually 4-spored, rarely 1-spored.

Over five hundred species chiefly epixylous, although some are humus-loving.

KEY TO GENERA OF Hydnaceæ

- | | |
|--|-----------------------------------|
| Sporophore annual; hymenium with more
or less subulate teeth or spines, pileus
not clavaria-like, teeth free, mostly
fleshy, rounded; spores hyaline. | 1. Hydnum , p. 294. |
| Sporophore perennial, punky or woody
Upper surface smooth, or sulcate. . . . | 2. Echinodontium , p. 295. |
| Upper surface zonate. | 3. Steccherinum , p. 295. |

¹ Banker, H. J. A contribution to a revision of the North American Hydnaceæ. Torr. Bot. Cl. Mem. 12: 99, 1906.

Hydnum Linnæus (p. 293)

Sporophore cuticular, leathery, corky, woody or fleshy, variable in form, resupinate; pileus shelving or bushy branched; sporiferous region beset with spines which support the hymenium; basidia with 4 sterigmata; spores hyaline.

The species of this genus, between two hundred fifty and three hundred, are mostly saprophytes but a few are true parasites on woody plants.

H. erinaceus Bul.

Cap 5–30 cm. wide, white, then yellowish or somewhat brownish, the branches forming a dense head covered with teeth, fleshy; stem short and stout, 2–8 cm. long and thick or entirely lacking; teeth 3–10 cm. long, slender, densely crowded; spores globose, clear, 5–6 μ . The name refers to the appearance of the head.



FIG. 285.—Fruiting body of *Hydnum erinaceus* in a hollow log. After von Schrenk and Spaulding.

It is the cause of a white rot on many deciduous trees, chiefly oaks. The rotted wood is soft and mushy. Numerous large holes filled with masses of light yellowish, fluffy mycelium occur in the heart-wood. Sporophores are often absent on the rotted tree.

H. septentrionale Fr.

Sporophores in bracket-like clusters, up to 20–30 cm. wide by 50–80 cm. long, creamy-white in color, texture at first fleshy, becoming more fibrous; pileus often 3 cm. thick, upper surface almost plain, slightly scaly, all pilei united behind, teeth slender, often 12 mm. long.

On sugar maple, beech, elm, etc., causing rot of the heart-wood.

H. schiedermayeri Heuf. occurs on living apple trees.

H. coralloides Scop. is the cause of heart rot of fir, also of spruce and poplar.

Echinodontium Ellis & Everhart (p. 293)

Similar to *Hydnum* but differing in perennial habit.

E. tinctorium E. & E.

Spines brown, 1 cm. long, $1\frac{1}{2}$ –2 mm broad; cystidia subconic, reddish-brown, $20\text{--}30 \times 6\text{--}7 \mu$.

On living trunks of hemlock, *Pseudotsuga* and fir in north-western North America.

Steccherinum S. F. Gray (p. 293)

Perennial, pileate, sulcate, zonate, radiately subrugose; teeth wide, irregular.

S. ballouii Banker is the single economic species.

Campanulate to subdimidiate, more or less intricate, sessile, decurrent to pendent, $1\text{--}4 \times 1\text{--}5$ cm., laterally connate up to 10 cm.; surface velutinous when young, often licheniferous at base, dark olive-brown, drying gray-brown in older parts and seal-brown in younger; margin obtuse, seal-brown; substance thin, 1–2 mm., of two layers, the upper harder, somewhat brittle, dark brown, lower softer and lighter colored; hymenium colliculose, golden-yellow, fading to buff or cream; teeth variable, subterete to difform, confluent, papaloid to elongate, usually obtuse, tips brownish, $1\text{--}5 \times 0.5\text{--}1$ mm., irregularly distributed; spores hyaline, broadly elliptic to subglobose, $7\text{--}7.2 \times 5.5\text{--}6.5 \mu$.

On *Chamaecyparis* in New Jersey. According to Ballou this fungus is devastating the forests of swamp cedar in New Jersey. As it grows only in the tops of the tree and dies with the host, the dead sporophores soon disappearing, it is a species not easily observed.

Polyporaceæ (p. 286)

Sporophore annual or perennial; context fleshy, tough, corky or woody; hymenium poroid or lamelloid, fleshy to woody, rarely gelatinous.

The sporophores are sometimes fleshy, even edible, but they are more commonly hard and woody, occurring as bracket forms, Fig. 296. on tree trunks.

KEY TO GENERA OF *Polyporaceæ*

- Pores well developed, variable in size and form **Polyporeæ.**
 Sporophore leathery, corky or punky, never gelatinous. Pores minute and rounded or large and angular
 Sporophore resupinate, never shelving 1. *Poria*, p. 296.
 Sporophore normally pileate, only accidentally resupinate
 Pores usually small or medium sized and round
 Substance of the pileus not continuing between the pores
 Sporophore at first fleshy, then hardening 2. *Polyporus*, p. 297.
 Sporophore from the first leathery or spongy, usually annual 3. *Polystictus*, p. 304.
 Sporophore from the first more or less corky or punky, usually perennial 4. *Fomes*, p. 305.
 Substance of the pileus continued between the pores 5. *Trametes*, p. 314.
 Pores usually large, hexagonal or labyrinthiform, rarely bounded by large plates
 Pores hexagonal
 Stipe lateral; pores elongate 6. *Favolus*, p. 315.
 Pores labyrinthine or replaced by plates
 Sporophore sessile
 Hymenium labyrinthine, becoming irpiciform 7. *Dædalea*, p. 316.
 Hymenium lamellate, not becoming irpiciform 8. *Lenzites*, p. 317.

Poria Persoon ¹

Sporophore entirely resupinate, often widely extended, the base leathery to punky, pores small, rounded, covering almost the entire surface.

A genus of about three hundred species.

P. lævigata Fr. causes a white rot of the birch.

P. vaporaria (Pers.) Fr. is a wound parasite on coniferous trees, especially common on spruce and fir causing a brown rot of the sap wood.

¹ Overholts, L. O. Diagnosis of American *Porias*. *Mycol.* **14**: 1, 1922.

P. subacida Pers. Sporophore effused, determinate; margin pubescent, white; pores minute, subrotund, 2–6 mm., oblique, odor subacid. A common saprophyte on deciduous and coniferous trees, especially pine, hemlock, and spruce. Irregular cavities form within the diseased wood and become lined with a tough felt of hyphæ, yellow on the inner side.

P. weirii Murr. is injurious on western red cedar (*Thuja*).

Polyporus (Micheli) Paulet (p. 296)

Sporophore usually annual; simple or compound, rather thick, fleshy, leathery or corky, stipitate or shelving, pores developing from the base toward the margin. Grading into *Polystictus* on the one hand and approaching *Fomes* on the other.

There are about five hundred species.

P. obtusus Berk.

Pileus somewhat imbricate, large and spongy, at length indurate, dimidiate, sessile, often ungulate, 5–7 x 10–15 x 3–5 cm.; surface spongy-tomentose, hirtose, azonate, smooth, sordid-white to isabelline or fulvous; margin very thick and rounded, sterile, entire, concolorous; context spongy-fibrous, white, indurate with age especially below, 1–2 cm. thick; tubes very long, 2–3 cm., white isabelline within, mouths large, irregular, often sinuous, 1–2 mm. broad, edges thin, fimbriate-dentate to slightly lacerate, white to isabelline, at length bay and resinous in appearance; spores globose, smooth, hyaline, 6–8 μ ; hyphæ hyaline, 6 μ ; cystidia none. It causes a heart-rot of living oaks, occurring as a wound parasite and invading the sap wood when decay is well advanced. It is also found on black locust.

P. sulphureus (Bul.) Fr.

Hymenophore cespitose-multiplex, 30–60 cm. broad; pileus cheesy, not becoming rigid, reniform, very broad, more or less stipitate, 5–15 x 7–20 x 0.5–1 cm.; surface finely tomentose to glabrous, rugose, anoderm, subzonate at times, varying from lemon-yellow to orange, fading out with age; margin thin, fertile, concolorous, subzonate, finely tomentose, undulate, rarely lobed; context cheesy, very fragile when dry, yellow when fresh, usually white in dried specimens, homogenous, 3–7 mm. thick; tubes annual, 2–3 mm. long, sulphur-yellow within; mouths minute, angular, somewhat irregular, 3–4 to a mm., edges very thin, lacerate, sulphur-yellow, with color fairly permanent in dried

specimens; spores ovoid, smooth or finely papillate, hyaline, $6-8 \times 3-5 \mu$.

It is common as a cause of red heart-rot of forest and shade trees, conifers and deciduous, and also does damage in the orchard, especially on cherry, apple and pear, and in the forest to oak, chestnut, poplar, maple, walnut, butternut, alder, locust, ash, pine, hemlock, larch.



FIG. 286.—*Polyporus sulphureus*. Scattered fruit bodies on living oak. After Atkinson.

The decayed wood resembles a mass of red-brown charcoal and is characterized by radial or concentric cracks in which the fungus forms thin leathery sheets. In dicotyledons the vessels become filled with the fungus. Round goniidia are often formed within the wood.

P. squamosus (Huds.) Fr.

Sporophore of immense size, reaching 50 cm. in breadth and 3 cm. in thickness, usually found in imbricated masses projecting from the trunks of living trees. Pileus subcircular and umbilicate when young, soon becoming flabelliform and explanate; surface ochraceous to fulvous, covered with broad, appressed, darker scales which are very close together in young specimens; margin involute, thin, entire; context fleshy-tough, juicy, milk-white, very thick, odor strong; tubes decurrent, white or pale yellowish, very short, mouths large, alveolar, 1 mm. or more in diameter, edges thin at maturity, toothed at an early age, becoming lacerate; spores broadly ovoid, smooth, hyaline, $5 \times 12 \mu$; stipe excentric to lateral, obese, reticulate above, clothed at the base with short, dark brown or black, velvety tomentum, often reduced, variable in length.

The mycelium causes white rot of nut, ornamental and fruit trees, particularly maple, pear, oak, elm, walnut, linden, willow, ash, birch, chestnut, beech, growing on dead parts of living trees. The hyphae advance most rapidly along the wood vessels and often bear clamp connections.

A biological study has been published by Buller who states that a single sporophore may produce 11,112,500,000 spores and that "the number produced by a single fungus from a single tree in the course of a year may, therefore, be some fifty times the population of the globe."

He showed the following enzymes to be present in the sporo-

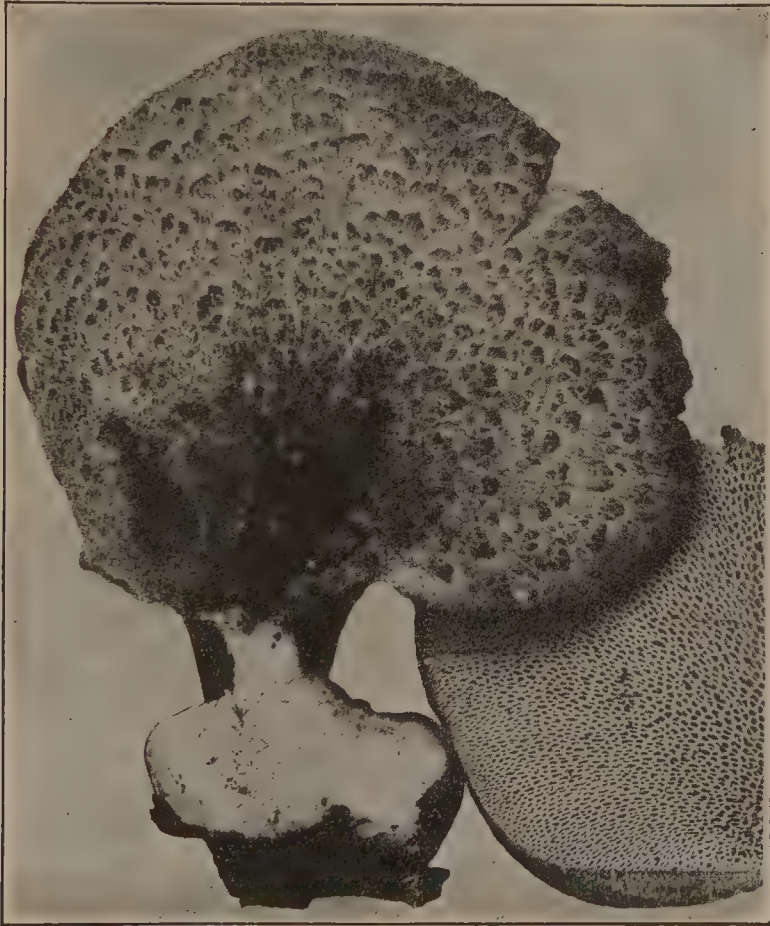


FIG. 287.—*Polyporus squamosus*. After Lloyd.

phore: laccase, tyrosinase, amylase, emulsin, protease, lipase, rennetase, and coagulase. Pectase, maltase, invertase, trehalase and cytase were not found; it is evident, however, that the mycelium in wood produces cytase and possibly hadromase.

***P. hispidus* Bul.**

Pileus thick, compact, fleshy to spongy, dimidiate, sometimes

imbricate, compressed-ungulate, 7-10 x 10-15 x 3-5 cm.; surface hirsute, ferruginous to fulvous, azonate, smooth; margin obtuse, velvety; context spongy-corky, somewhat fragile when dry, ferruginous to fulvous, blackening with age, 1-1.5 cm. thick; tubes slender, about 1 cm. long, ferruginous within, mouths angular, 2-3 to a mm., ferruginous to bay, blackening with age, edges thin, very fragile, lacerate; spores broadly ovoid, smooth, thick-walled, deep-ferruginous, 2 guttulate, 5-6 x 7-8 μ .

It is common on all kinds of deciduous trees, often injuring fruit trees, especially the apple.

P. giganteus (Pers.) Fr. has been reported as injurious to the oak and is also on conifers.

P. gilvus Fr. is a common saprophyte on deciduous trees and juniper and in some cases may be parasitic.

P. dryophilus Berk.

Pileus thick, unequal, unguliform, subimbricate, rigid, 7-8 x 10-14 x 2-3 cm.; surface hoary-flavous to ferruginous-fulvous, becoming scabrous and bay with age; margin thick, usually obtuse, sterile, pallid, entire or undulate; context ferruginous to fulvous, zonate, shining, 3-10 mm. thick; tubes slender, concolorous with the context, about 1 cm. long, mouths regular, angular, 2-3 to a mm., glistening, whitish-isabelline to dark-fulvous, edges thin, entire to toothed; spores subglobose, smooth, deep-ferruginous, 6-7 μ ; cystidia scanty and short; hyphæ deep-ferruginous.

It causes a piped rot of oaks, and occurs also on poplar.

P. borealis (Wahl.) Fr.

Pileus sessile, subimbricate, dimidiate to flabelliform, often narrowly attached, spongy to corky, very tough, moist and juicy when fresh, 5-8 x 8-12 x 2-4 cm.; surface uneven, soft and spongy, hirtose-tomentose, azonate, white to yellowish; margin thin, white, entire, somewhat discolored on drying; context fibrous-coriaceous above, fibrous-woody below, white, 0.5-1.5 cm. thick; tubes 4-8 mm. long, white to pallid within, mouths angular, irregular, somewhat radiately elongate, sinuous at times, 1-2 to a mm., stuffed when young, edges thin, white to ochraceous, dentate to lacerate; spores ovoid, smooth, hyaline, 5-6 x 3-4 μ ; hyphæ 6-7 μ ; cystidia none.

On pine, spruce, hemlock, balsam, pine, etc., as a wound parasite or as a saprophyte on dead trees producing a white rot. The mycelium advances longitudinally, radially and tangentially. At certain stages it is very abundant and forms cords in the channels

formed by the fungous enzyme. Later these cords disappear. The young mycelium is stout and yellow, later it is more delicate. Dissolution of the cells begins at the lumen and proceeds outward, the middle lamella persisting last.

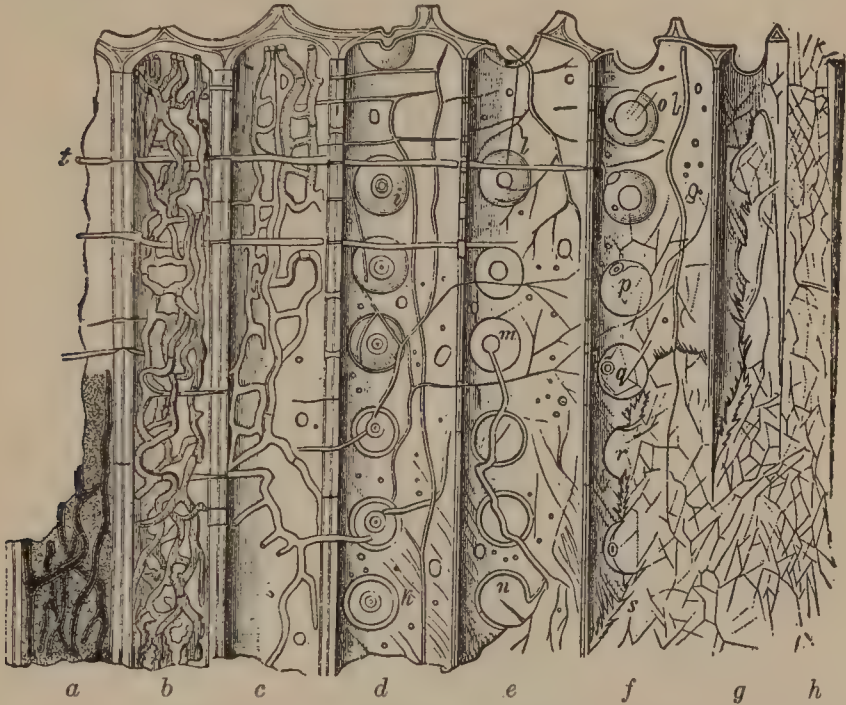


FIG. 288.—Decomposition of spruce-timber by *Polyporus borealis*. *a*, a tracheid containing a strong mycelial growth and a brownish yellow fluid which has originated in a medullary ray; at *b* and *c* the mycelium is still brownish. At *d* and *e* the walls have become attenuated and perforated, the filaments delicate; at *f* the pits are almost destroyed; at *g* and *h* only fragments of the walls remain. The various stages in the destruction of the bordered pits are to be followed from *i* to *r*; at *i* the bordered pit is still intact; at *k* the walls of the lenticular space have been largely dissolved, their inner boundary being marked by a circle; at *l* one side of the bordered pit has been entirely dissolved; at *m* and *n* one sees a series of pits which have retained a much-attenuated wall on one side—namely, on that which is provided with the closing membrane. In making the section a crack has been formed in this wall. Between *o* and *r* both walls of the pits are found to be wholly or partially dissolved, only at *p* and *q* has the thickened portion of the closing membrane been preserved; at *d* the spiral structure of both cell-walls is distinctly recognizable. These walls when united form the common wall of the tracheid; at *t* hyphae are seen traversing the tracheids horizontally. After Hartig.

P. dryadeus Pers. Fr. is a root parasite of oak.

P. amarus Hedg.

Pileus soft and spongy when young, becoming hard and chalky when old, ungulate, often spuriously stipitate from knot-holes, frequently large, 5–11 x 10–20 x 6–12 cm.; surface pubescent when young, rimose and chalky when old, at first buff, becoming tan and often blotched with brown when older; margin obtuse, fre-

quently having an outer band of darker brown, often slightly furrowed; context creamy-yellow to tan-colored, usually darker in outer layers when old, 4–8 cm. thick; tubes not stratified, brown within, cylindric, 0.5–3 cm. in length, shorter next the margin, mouths circular or slightly irregular, 1–3 to a mm., yellow-green during growth, turning brown when bruised or old, becoming

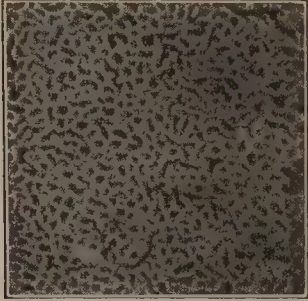


FIG. 289.—*Polyporus borealis*, hymenium with sinuous pores. After Atkinson.

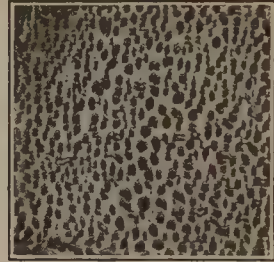


FIG. 290.—*Polyporus borealis*, hymenium with rounded pores. After Atkinson.

lacerate; spores hyaline or slightly tinged with brown, smooth, ovoid, $3-4 \times 5-8 \mu$, nucleated; cystidia none.

The cause of "pin rot" or peckiness of incense cedar.

***P. schweinitzii* Fr.**

Pileus spongy, circular, varying to dimidiate or irregular, 15–20 cm. broad, 0.5–2 cm. thick; surface setose-hispid to strigose-tomentose and scrupose in zones, ochraceous-ferruginous to fulvous-castaneous or darker, quite uneven, somewhat sulcate, obscurely zonate; margin yellow, rather thick, sterile: context very soft and spongy, fragile when dry, sometimes indurate with age, flavous-ferruginous to fulvous, 0.3–0.7 mm. thick; tubes short, 2–5 mm. long, flavous within, mouths large, irregular, averaging 1 mm. in diameter, edges thin, becoming lacerate, ochraceous-olivaceous to fuliginous, rose-tinted when young and fresh, quickly changing to dark-red when bruised: spores ovoid, hyaline, $7-8 \times 3-4 \mu$; stipe central to lateral or obsolete, very irregular, tubercular or very short, resembling the pileus in surface and substance.

On coniferous trees, especially spruce, fir, pine, larch, arbor vitæ, entering through the root system and extending up the trunk, causing heart-rot. The tracheids exhibit spiral cracks and fissures due to the shrinking of the walls. Fig. 279. Diseased wood is yellowish and of cheesy consistency; brittle when dry.

***P. betulinus* (Bul.) Fr.**

Pileus fleshy to corky, compressed-ungulate, convex above, plane below, attached by a short umbo behind, varying to bell-shaped when hanging from horizontal trunks, 5-30 x 5-20 x 2-5



FIG. 291.—A dead, yellow birch tree with fruiting body of *P. betulinus*. After von Schrehk and Spaulding.

cm.; surface smoky, covered with a thin, separating pellicle, glabrous, devoid of markings, cracking with age; margin velvety, concolorous, obtuse, projecting nearly a centimeter beyond the hymenium; context fleshy-tough, elastic, homogenous, 3 cm. thick, milk-white; tubes 0.5 cm. long, 2-3 to a mm., sodden-white, sepa-

rated from the context by a thin pink layer; mouths very irregular, dissepiments thicker than the pores, obtuse, entire, crumbling away in age, leaving the smooth, white context; spores white, cylindrical, curved, 4–5 μ in length. The mycelium penetrates lignified cell walls entering the living cells and causing death.

On birch it causes a decay of the sap wood similar to that caused by *Fomes fomentarius*.

P. adustus (Wild.) Fr. is a common saprophyte of deciduous trees.

Numerous other species occur on oak, larch, chestnut, chinquapin, poplar, spruce, fir, juniper and many other conifers and deciduous trees.

Polystictus Fries (p. 296)

Sporophore leathery, usually thin; pores developing from the center to the circumference of the hymenophore. The thicker forms are quite close to some species of *Polyporus*.

About four hundred fifty species.

P. versicolor (L.) Fr.

Pileus densely imbricate, very thin, sessile, dimidiate, conchate, 2–4 x 3–7 x 0.1–0.2 cm.; surface smooth, velvety, shining, marked with conspicuous, glabrous zones of various colors, mostly latericeous, bay or black; margin thin, sterile, entire; context thin, membranous, fibrous, white; tubes punctiform, less than 1 mm. long, white to isabelline within, mouths circular to angular, regular, even, 4–5 to a mm., edges thick and entire, becoming thin and dentate, white, glistening, at length opaque-isabelline or slightly umbrinous; spores allantoid, smooth, hyaline, 4–6 x 1–2 μ ; hyphæ 2–6 μ ; cystidia none.

Von Schrenk regards this as strictly a saprophyte except when on catalpa, where it causes a heart-rot. It is common on almost any kind of wood.

Catalpa wood under its action becomes straw-colored and finally soft and pithy. Both cellulose and lignin are dissolved.

P. sanguineus (L.) Fr. and **P. cinnabarinus** (Jacq.) Fr. are saprophytes on dead parts of live trees.

P. velutinus (Pers.) Fr. is a common saprophyte which is perhaps sometimes parasitic.

P. pergamenus Fr.

Pileus exceedingly variable, sessile or affixed by a short tubercle, dimidiate to flabelliform, broadly or narrowly attached, 2–5 x 2–6

x 0.1–0.3 cm.; surface finely villose-tomentose, smooth, white or slightly yellowish, marked with a few narrow indistinct latericeous or bay zones; margin thin, sterile, entire to lobed; context very thin, white, fibrous; tubes 1–3 mm. long, white to discolored within, mouths angular, somewhat irregular, 3–4 to a mm., usually becoming irpiciform at an early stage, edges acute, dentate, becoming lacerate, white to yellowish or umbrinous; spores smooth, hyaline.

It causes a sapwood rot of practically all species of deciduous trees, often on dead trees, less frequently on living trees which have been severely injured. In general the rotten wood resembles that produced by *P. versicolor*; microscopically it is seen that the fungus attacks chiefly the lignin.

***P. hirsutus* Fr.**

Pileus confluent-effused, more or less imbricate, sessile, dimidiate, applanate, corky-leathery, rather thick, flexible or rigid, 3–5 x 5–8 x 0.3–0.8 cm.; surface conspicuously hirsute, isabelline to cinereous, concentrically furrowed and zoned; margin at length thin, often fuliginous, sterile, finely strigose-tomentose, entire or undulate; context white, thin, fibrous, spongy above, 1–4 mm. thick; tubes white, 1–2 mm. long, mouths circular to angular, 4 to a mm., quite regular, edges thin, firm, tough, entire, white to yellowish or umbrinous; spores smooth, hyaline, cylindrical, slightly curved, 2.5–3 μ . On deciduous trees and conifers; a wound parasite of the mountain ash.



FIG. 292.—*Polystictus pergamenus*. After Freeman.

Fomes Fries (p. 296)

Sporophore sessile, ungulate or applanate; surface varnished, encrusted, sulcate, vinose, or anoderm, rarely zonate; context

corky to punky; tubes cylindric, stratiöse; spores smooth, hyaline or brown.

A genus of some three hundred species.

***F. igniarius* (L.) Gill.**

Pileus woody, ungulate, sessile, 6-7 x 8-10 x 5-12 cm.; surface smooth, encrusted, opaque, velvety to glabrous, ferruginous to fuscous, becoming rimose with age; margin obtuse, sterile, ferruginous to hoary, tomentose; context woody, distinctly zonate, ferruginous to fulvous, 2-3 cm. thick; tubes evenly stratified, 2-4 mm. long each season, fulvous, whitish-stuffed in age, mouths circular, minute, 3-4 to a mm., edges obtuse, ferruginous to ful-

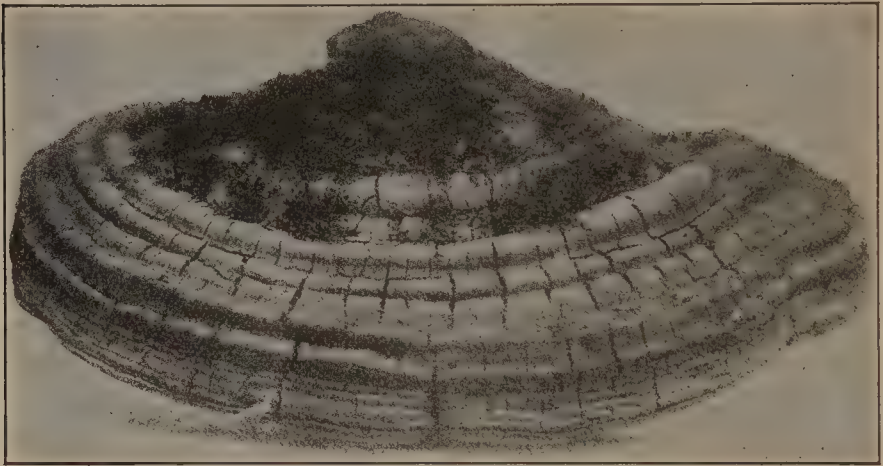


FIG. 293.—*Fomes igniarius*, from maple. After Atkinson.

vous, hoary when young; spores globose, smooth, hyaline, 6-7 μ ; spines 10-25 x 5-6 μ .

It is the cause of a white heart-rot, one of the most widely distributed forms of wound parasites, and occurs on more species of broad-leaf trees than any other similar fungus. Among its hosts are beech, oak, apple, peach, willow, aspen, the maples, birch, butternut, walnut, hickory, alder.

The first sporophores usually appear at the point of initial infection. The mycelium grows mainly in the heart wood but it may gain entrance through the sap wood or enroach upon the sap wood from the heart wood. Its growth may continue after the death of the host. In early stages it follows the medullary rays. The completely rotted wood is white to light yellow and in it the mycelium abounds in the large vessels and the medullary

rays. The walls of the affected wood cells are thin and the middle lamella is often wholly lacking, due to solution of the lignin.

***F. fomentarius* (L.) Fr.**

Pileus hard, woody, ungulate, concave below, 7-9 x 8-10 x 3-10 cm.; surface finely tomentose to glabrous, isabelline to avellaneous



FIG. 294.—A dead beech tree with sporophores of *F. fomentarius*. After von Schrenk and Spaulding.

and finally black and shining with age, zonate, sulcate, horny-encrusted; margin obtuse, velvety, isabelline to fulvous; context punky, homogeneous, ferruginous to fulvous, conidia-bearing, 3-5 mm. thick; tubes indistinctly stratified, not separated by layers of context, 3-5 mm. long each season, avellaneous to umbrinous within, mouths circular, whitish-stuffed when young, 3-4 to a mm.;

edges obtuse, entire, grayish-white to avellaneous, turning dark when bruised; spores globose, smooth, very light brown, 3–4 μ ; hyphæ brown, 7–8 μ ; cystidia none.

The mycelium kills the cambium and causes a white rot of the sap wood of deciduous trees, especially beech, birch, elm, maple, reported also on apple. The wholly rotted wood is soft and spongy, light yellow and crumbles into its separate fibers.

F. everhartii E. & G. (= *Pyropolyporus prærimosa*)

Pileus woody, dimidiate, unguulate, broadly attached behind, 6–10 x 6–15 x 3–8 cm.; surface glabrous, slightly encrusted, deeply sulcate, not polished, gray to brownish-black, slightly rimose in age; margin obtuse, covered with ferruginous tomentum, becoming gray and glabrous; context corky to woody, repeatedly zoned, fulvous in dried specimens, 2–3 cm. thick; tubes evenly stratified, 0.5–1 cm. long each season, fulvous, mouths circular, 4 to a mm., edges rather thin, entire, ferruginous to fulvous, glistening, the hymenium becoming much cracked in age; spores globose, smooth, ferruginous, 3–4.5 μ ; spines abundant, pointed, larger at the base, 15–25 x 6–10 μ .

On black oaks and walnuts causing a rot almost indistinguishable from that caused by *F. igniarius*. The mycelium often grows into the living sap wood.

F. carneus Nees

Pileus woody, dimidiate, varying from conchate to unguulate, often imbricate and longitudinally effused, 2–4 x 6–8 x 0.5–3 cm.; surface rugose, subfasciate, slightly sulcate, rosy or flesh-colored, becoming gray or black with age; margin acute, becoming obtuse, sterile, pallid, often undulate; context floccose-fibrose to corky, rose-colored, 0.2–2 cm. thick; tubes indistinctly stratose, 1–2 mm. long each season, mouths circular, 3–4 to a mm., edges obtuse, concolorous; spores ellipsoid, smooth, thick-walled subhyaline, 3.5 x 6 μ .

On red cedar and arbor vitæ causing pockets, also on dead spruce and fir. The cellulose is almost all removed from the affected cells of the heart wood. The mycelium is scant and when young is pale and with numerous clamps. It extends horizontally through the tracheids, giving off lateral branches. None is found in the sap wood.

F. annosus (Fr.) Cke. (= *Trametes radiciperda* R. Hartig)

Pileus woody, dimidiate, very irregular, conchate to applanate, 10–13 x 5–8 x 0.5–2 cm.; surface at first velvety, rugose, anoderm,

light brown, becoming thinly encrusted, zonate, and finally black with age; margin pallid, acute, becoming thicker; context soft-corky to woody, white, 0.3–0.5 cm. thick; tubes unevenly stratified, 2–8 mm. long each season, white, mouths subcircular to irregular, 3–4 to a mm., edges rather thin, entire, firm, white, unchanging; spores subglobose or ellipsoid, smooth, hyaline, 5–6 x 4–5 μ .

On pine, fir and various deciduous trees, including apple, described by Hartig as the most dangerous of all conifer parasites. It is not so plentiful in America as in Europe.

The sporophores appear near or on the roots, between the bark scales, where the white felted delicate mycelium also occurs. The spores, carried presumably by rodents, germinate upon the bark of roots; the mycelium penetrates to the living cortex, forces its way into the wood and follows up the stem and down the root. The parenchyma cells are killed and browned; the wood becomes violet, later brownish-yellow. The hyphæ travel in the cell lumen and pierce the walls. The lignified parts are dissolved first, later the middle lamella disappears. Eventually the whole root system may become involved and the death of the tree result.

F. juniperinus (v. Sch.) S. & Sy.

Pileus woody, ungulate, 3–5 x 5–8 x 5–7 cm; surface tomentose, deeply sulcate, ferruginous to gray, at length rough and grayish-black; margin obtuse, velvety, melleous or ferruginous to hoary; context corky to woody, reddish-fulvous, 0.5–1 cm. thick; tubes indistinctly stratified, 0.5–1 cm. long each season, melleous within, reddish-fulvous in the older layers, mouths circular to angular, 2–3 to a mm., edges rather thin, entire, even, melleous; spores reddish-brown, smooth; spines blunt, only slightly projecting. On red cedar.

In the holes caused by the fungus in the heart wood is found a velvety mass of reddish-yellow mycelium, glistening with colorless liquid and holding masses of reddish-brown wood fiber. Long white fibers of cellulose with the lignin removed project into the cavities from the ends.

Structural change begins soon after the mycelium enters a cell lumen. The primary lamella becomes granular and is dissolved by a lignin-splitting enzyme, the secondary lamella becomes white and the cells fall apart.

The mycelium in newly invaded tissue is nearly hyaline and extends lengthwise. Within the tracheids branches are given off in all directions.

The sporophore appears after decomposition is considerably advanced.

F. laricis (Jacq.) Murr.

Pileus firm, at length fragile, ungulate to cylindrical, 3-8 x 5-10 x 4-20 cm.; surface anoderm, powdery, white or slightly yellowish, concentrically sulcate, becoming slightly encrusted, tuberculose and rimose; margin obtuse, concolorous; context soft, tough, at length friable, chalk-white or slightly yellowish, very bitter, with the odor of fresh meal, 1-3 cm. thick; tubes evenly stratified, concolorous, 5-10 mm. long each season, mouths circular to angular, 3-4 to a mm., edges thin, fragile, white, becoming discolored and lacerate, wearing away with age; spores ovoid, smooth, hyaline, 4-5 μ ; hyphæ 5 μ ; cystidia none.

A wound parasite of the larch, pine and spruce in Europe and America.

F. ribis (Schw.) Gill.

Pileus tough, corky, becoming rigid, conchate, laterally connate, 3-5 x 5-10 x 0.7-1.5 cm.; surface rough, velvety, anoderm, indistinctly zoned, ferruginous to umbrinous, becoming glabrous and slightly encrusted with age; margin undulate to lobed, ferruginous, furrowed; context punky, fulvous, 3-5 mm. thick; tubes indistinctly stratified, 1-2 mm. long each season, fulvous, mouths circular, 5-6 to a mm., edges rather thin, entire, ferruginous to fulvous, hoary when young; spores globose or subglobose, pale yellowish-brown, smooth, 3-4 x 3 μ ; hyphæ 2.5 μ ; cystidia none.

This is a wound parasite on the heart wood of sassafras and is also found on roots and stems of various shrubby plants including rose, gooseberry and currant. The fungus fills the large vessels and tracheids with a brown mycelium and dissolves the entire wall locally.

F. fulvus (Scop.) Gill.

Pileus woody, triquetrous, rarely ungulate, thick and broadly attached behind, 1-3 x 5-7 x 3-8 cm.; surface smooth, very slightly sulcate, velvety, ferruginous, becoming horny and glabrous and finally nearly black with age; margin subobtuse, ferruginous, velvety; context woody, fulvous, 1-2 cm. thick; tubes evenly stratified, 2-3 mm. long each season, fulvous, mouths circular, 3 to a mm., edges obtuse, entire, ferruginous to fulvous; spores globose, compressed on one side, hyaline, 5.5-6 x 4.5-5 μ ; spines fulvous, 15-20 x 7-9 μ ; hyphæ 2.5 μ .

On plum, birch and other trees.

The decayed wood is red-brown and crumbles when crushed.

F. nigricans Fr. is very similar to *F. igniarius* from which it differs chiefly in the black upper surface and the bluish or blackish hymenial surface of the sporophores.

As a wound parasite it causes a reddish-brown heart-rot of deciduous trees, especially of willow, birch, poplar, beech.

F. fraxinophilus (Pk.) Sacc.

Pileus woody, subtriangular, compressed-ungulate, usually decurrent, 5–10 x 6–12 x 2–4 cm.; surface white, pulverulent or finely tomentose, concentrically sulcate, becoming gray or black and rimose with age; margin tumid, white or yellowish, velvety to the touch; context corky to woody, zonate, isabelline, 0.5–1 cm. thick; tubes evenly but indistinctly stratified, 2–4 mm. long each season, white when young, concolorous with the context in the older layers, mouths white, subcircular, 2 to a mm., edges obtuse; spores broadly ellipsoid, smooth, hyaline, thin-walled, 6–7 x 7–8 μ ; hyphæ light yellowish-brown, 10–12 μ ; cystidia none.

It causes a heart-rot of trunk and branches of species of ash.

The starch in the host cells is lost early by diastatic action in advance of the fungus, the nearest hyphæ of which may be several millimeters distant, and is replaced by a decomposition product. The mycelium advances through the medullary rays and spreads through spring and summer bands, abstracting the lignin; the middle lamella dissolves and the cells fall apart. Completely rotted wood is straw-colored, very soft, non-resistant. The young hyphæ are very fine and require an immersion lens for observation. Clamp connections are frequent. The sporophore appears after the destruction of the wood is considerably advanced.

F. robiniae (Murr.) S. & Sy.

A large fungus with dark rimose surface and tawny hymenium. Pileus hard, woody, dimidiate, ungulate to applanate, 5–25 x 5–50 x 2–12 cm.; surface velvety, smooth, soon becoming very rimose and roughened, fulvous to purplish-black, at length dull-black, deeply and broadly concentrically sulcate; margin rounded, velvety, fulvous; context hard, woody, concentrically banded, 1–3 cm. thick, fulvous; tubes stratose, 0.15–0.5 cm. long, 50 to a mm., fulvous, mouths subcircular, edges entire, equaling the tubes in thickness; spores subglobose, smooth, thin-walled, ferruginous, copious, 4–5 μ ; cystidia none.

On black locust causing heart-rot, arising from wound infection of living trees. The very hard wood becomes a soft, yellow to

brown mass, spongy when wet. The decay extends out in radial lines from the center, along the large medullary rays, killing the cambium and bark on reaching them. The lignin is first dissolved, later the cellulose.

The fungus ceases growth on the death of its host.

F. marmoratus Berk. (= *F. fasciatus* [Sw.] Cke.)

Pileus hard, woody, dimidiate, applanate to unguulate, convex above, 7–10 x 8–15 x 2–6 cm.; surface finely tomentose, at length glabrous, concentrically sulcate, at first mole-colored, changing to umbrinous, and finally avellaneous with black fasciations; margin acute to obtuse, isabelline, sterile, undulate or entire; context punky, thin, ferruginous to fulvous, zonate, 3–5 mm. thick, tubes indistinctly stratified, 5–10 mm. long each season, avellaneous within, mouths circular, minute, 4–5 to a mm., edges obtuse, avellaneous to umbrinous, becoming darker when bruised; spores subglobose, smooth, light brown, 5–7 μ ; hyphæ brown, 4–6 μ ; cystidia none.

On water oak and orange, especially abundant on the former.

F. sessilis (Murr.) Sacc.

A variable fungus with wrinkled varnished cap and acute margin, found on decaying deciduous trees. Pileus corky to woody, dimidiate, sessile or stipitate, imbricate or connate at times, conchate to fan-shaped, thickest behind, thin at the margin, 5–15 x 7–25 x 1–3 cm.; surface glabrous, laccate, shining, radiate-rugose, concentrically sulcate, yellow to reddish-chestnut, at length opaque, dark-brown, usually marked near the margin with alternating bay and tawny zones; margin usually very thin and acute, often curved downward, often undulate, rarely becoming truncate, white, at length concolorous; context soft-corky or woody, radiate-fibrous, concentrically banded, ochraceous-fulvous; tubes 0.52 cm. long, 3–5 to a mm., brown within, mouths circular or angular, white or grayish-brown, edges thin, entire; spores ovoid, obtuse at the summit, attenuate and truncate at the base, verrucose, yellowish-brown, 9–11 x 6–8 μ ; stipe laterally attached, usually ascending, irregularly cylindrical, 1–4 x 0.5–1.5 cm., resembling the pileus in color, surface and substance, often obsolete.

It occurs on oak and maple as a wound parasite, destroying bark and cambium. This and related species are usually saprophytic.

F. pinicola Fr.

Pileus corky to woody, unguulate, 8–15 x 12–40 x 6–10 cm.; surface glabrous, sulcate, reddish-brown to gray or black, often

resinous; margin at first acute to tumid, pallid, becoming yellowish or reddish-chestnut; context woody, pallid, 0.5–1 cm. thick; tubes distinctly stratified, 3–5 mm. long each season, white to isabel-line, mouths circular, 3–5 to a mm., edges obtuse, white to cream-colored; spores ovoid, smooth, hyaline, $6\ \mu$; hyphæ $8\ \mu$; cystidia none.

It occurs on conifers; pine, hemlock, spruce, balsam, larch, etc., more rarely on beech, birch and maple, as a wound parasite of the heart wood. The sporophores are often absent until after death of the host. The tracheids bear many holes. The wood carbonizes, the cellulose is destroyed and sheets of mycelium form, particularly within the space occupied by the medullary rays and in tangential crevices. Fig. 295.

F. applanatus (Pers.) Wallr.

Pileus hard, woody, dimidiate, applanate, 6–15 x 8–30 x 1–4 cm.; surface milk-white to gray or umbrinous, glabrous, concentrically sulcate, encrusted, fasciate with obscure lines, conidia-bearing, usually brownish during the growing season from the covering of conidia; margin obtuse, broadly sterile, white or slightly cremeous, entire to undulate; context corky, usually rather hard, zonate, fulvous to bay, 5–10 mm. thick, thinner with age; tubes very evenly stratified, separated by thin layers of context, 5–10 mm. long each season, avellaneous to umbrinous within, mouths circular, 5 to a mm., whitish-stuffed when young, edges obtuse, entire, white or slightly yellowish to umbrinous, quickly changing color when bruised; spores ovoid, smooth or very slightly roughened, pale yellowish-brown, truncate at the base, $7\text{--}8 \times 5\text{--}6\ \mu$.

It is described as the cause of rot of both heart and sap wood of living cotton-wood trees. The invaded medullary rays first



FIG. 295.—*F. pinicola* growing on dead trunk of western hemlock. After von Schrenk.

lose their starch by digestion. Next the lignin is dissolved, then the cellulose.



FIG. 296.—*Fomes applanatus*. After Freeman.

Trametes Fries (p. 296)

Sporophore annual, rarely perennial, sessile; context homogeneous, coriaceous to corky, extending between the tubes, which are circular or irregular.

There are about one hundred fifty species.

***T. pini* (Thore) Fr.**

Pileus hard, woody, typically ungulate, conchate or effused-reflexed in varieties, often imbricate, 5-8 x 7-12 x 5-8 cm., smaller in varieties; surface very rough, deeply sulcate, tomentose, tawny-brown, becoming rimose and almost black with age; margin rounded or acute, tomentose, ferruginous to tawny-cinnamon, entire, sterile in large specimens: context soft-corky to indurate, homogeneous, ferruginous, 5-10 mm. thick, thinner in small specimens; tubes stratified, white to avellaneous within, becoming ferruginous at maturity and in the older layers, 5 mm. long each season, much shorter in thin specimens; mouths irregular, circular or daedaloid, often radially elongate, averaging 1 to a mm., edges ferruginous to grayish-umbrinous, glistening when young, rather thin, entire; spores subglobose, smooth, hyaline at maturity, becoming brownish with age, 5-6 x 3-4 μ ; spines abundant, short, 25-35 x 4-6 μ .

It occurs on pine, spruce, larch, hemlock, and fir as a wound parasite of the heart wood; it is also on willow and birch.

The spores are wind-borne and, lodging on unprotected surfaces, develop a mycelium which grows both up and down, spreading most rapidly in a longitudinal direction, or horizontally following an annual ring. The fungous enzyme first dissolves the lignin leaving the individual tracheids free and of nearly pure cellulose. The cellulose is later dissolved, resulting in holes in the wood. It is found on most of the conifers of the United States as a saprophyte. The wood becomes white-spotted. In late stages of decay the entire wood is full of small holes which are lined with a white fungous felt.

***T. suaveolens* (L.) Fr.**

Pileus large, subimbricate, dimidiate, sessile, convex above, plane or concave below, 4-6 x 5-12 x 1-3 cm.; surface smooth, anoderm, azonate, finely villose-tomentose to nearly glabrous, white to pale-isabelline; margin thick, sterile, entire; context white, punky-corky, 1-2 cm. thick, very fragrant when fresh, with the odor of anise; tubes 5-15 mm. long, white within, mouths circular, 2 to a mm., edges at first very thick, white, entire, becoming thinner and often blackish with age; spores oblong-ovoid, subsinuate, smooth, hyaline, 8-9 x 3-5 μ ; hyphæ 7 μ ; cystidia none.

On willow and poplar.



FIG. 297.—*Favolus europæus*. After Lloyd.

***Favolus* Fries (p. 296)**

Sporophore leathery, fleshy, or coriaceous, laterally stipitate; hymenium with large elongated pores which may even become lamellate, Fig. 297.

A genus of some seventy species.

***F. europæus* Fr.** is a parasite of fruit and nut trees.

Dædalea Persoon (p. 296)

Hymenophore epixylous, usually large and annual, sessile, applanate to ungulate; surface anoderm, glabrous, often zonate; context white, wood-colored or brown, rigid, woody, tough or punky; hymenium normally labyrinthiform, but varying to lamellate and porose in some species; spores smooth, hyaline.

About seventy-six species. Fig. 298.

D. quercina (L.) Pers.

Pileus, corky, rigid, dimidiate, sessile, imbricate, applanate, convex below, triangular in section, 6–12 x 9–20 x 2–4 cm.; surface isabelline-avellaneous to cinerous or smoky-black with age, slightly sulcate, zonate at times, tuberculose to colliculose in the older



FIG. 298.—*Dædalea quercina* on oak. After von Schrenk and Spaulding.

portions; margin usually thin, pallid, glabrous; context isabelline, soft-corky, homogeneous, 5–7 mm. thick; tubes labyrinthiform, becoming nearly lamellate with age in some specimens, 1–2 cm. long, 1–2 mm. broad, chalk-white or discolored within, edges obtuse, entire, ochraceous to avellaneous.

Common on oak, maple and chestnut, often on living trees but growing only on the dead wood.

Lenzites Fries (p. 296)

Hymenophore small, annual, epixylous, sessile, conchate; surface anoderm, usually zonate and tomentose; context white or brown, coriaceous, flexible; hymenium lamellate, the radiating gill-like dissepiments connected transversely at times, especially when young; spores smooth, hyaline. Fig. 299.

About seventy-five species.

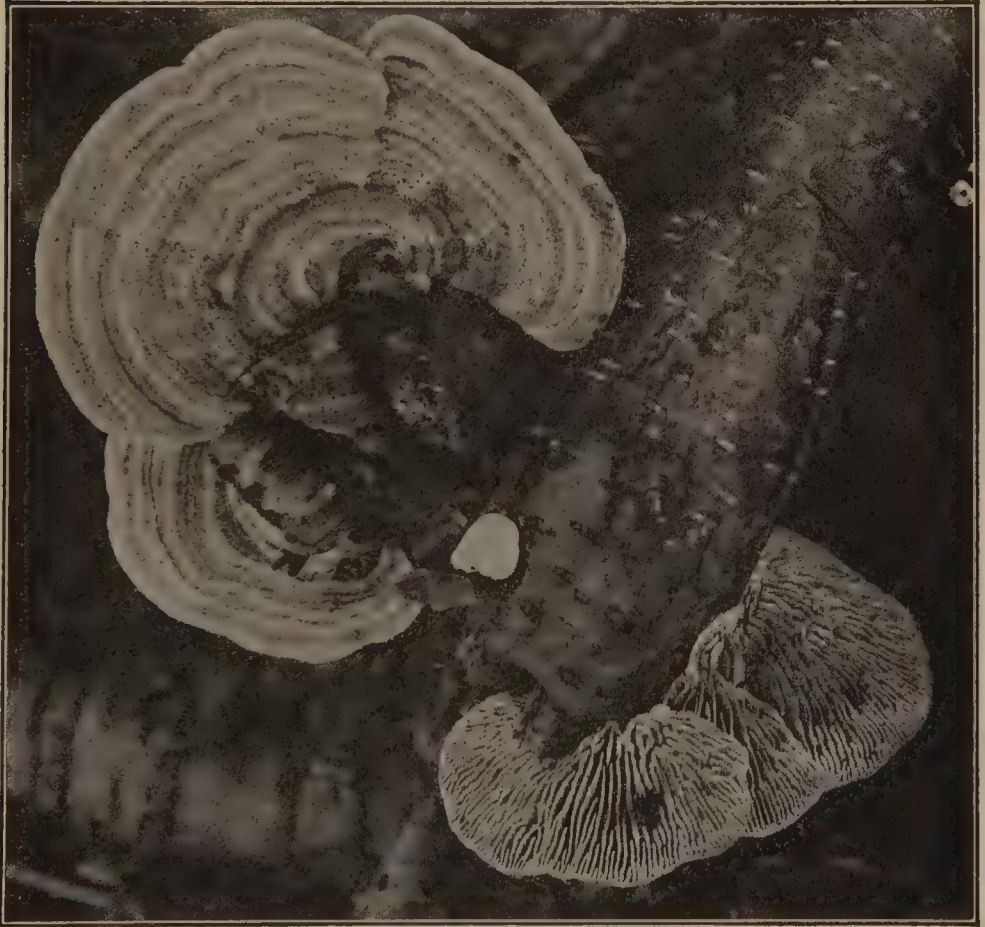


FIG. 299.—*Lenzites betulina*. After Freeman.

L. abietina (Bul.) Fr. occurs on firs. **L. sepiaria** (Wulf.) Fr. has been reported as a parasite on conifers and deciduous trees. **L. vialis** Pk. and **L. betulina** (L.) Fr. are common saprophytes on deciduous trees, perhaps also parasitic; **L. variegata** Fr. occurs on beech and poplar.

Agaricaceæ (p. 286)

Sporophores usually fleshy, rarely coriaceous or leathery, stipitate or shelving; stipe variable in development, lateral or central, annulate or not, the entire young sporophore often volvate at first; hymenium lamellate, the lamellæ usually free, rarely anastomosing, sometimes dichotomous, rarely reduced to ridges or slight folds.

A family of over twelve hundred species.

KEY TO TRIBES OF Agaricaceæ

- Hymenium with normally developed gills;
 lamellæ not fleshy or waxy; substance
 of the pileus of only one kind of hyphæ
 Sporophore at maturity leathery or corky,
 persistent, rarely fleshy
 Lamellæ at maturity split lengthwise. . . 1. **Schizophylleæ**, p. 318.
 Lamellæ at maturity not splitting. 2. **Marasmieæ**, p. 319.
 Sporophore at maturity fleshy, finally
 putrescent. 3. **Agariceæ**, p. 320.

Schizophylleæ

Sporophore, leathery, persistent, the cleft gills with recurved margins.

Schizophyllum Fries

Cap woolly, upturned, sessile, epixylous; gills cleft, the margins recoiled; texture leathery.

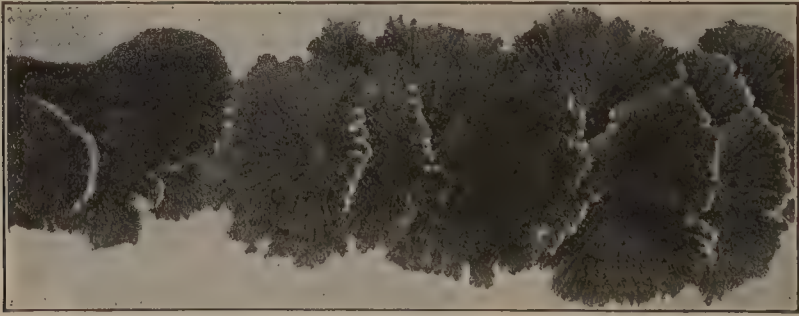


FIG. 300.—*S. alneum*. After Atkinson.

About twelve species. Fig. 300.

***S. alneum* (L.) Schr.**

Cap 1–4 cm. wide, white or gray-woolly, upturned, attached excentrically, irregularly saucer-shaped, stem lacking; gills grayish to purplish; spores subglobose, 2–3 μ .

It parasitizes sugar-cane, horse chestnut, chestnut, mulberry and orange.

Marasmieæ (p. 318)

Pileus tough, leathery, thin, membranous, or rarely somewhat fleshy, reviving after drying with the return of moisture.

About five hundred fifty species.

KEY TO GENERA OF **Marasmieæ**

Gills leathery; spores hyaline

Pileus not distinct from the stipe; sporophore trumpet-shaped; gills with a thin edge, toothed on the margin.....

1. **Lentinus**, p. 319.

Pileus distinct from the stipe; annulus wanting; pileus firm and dry.....

2. **Marasmius**, p. 320.

Lentinus Fries

Sporophore trumpet-shaped, pileus and stipe not distinct, leathery, pileus central or lateral, gills toothed; spores white.

About three hundred fifty species.

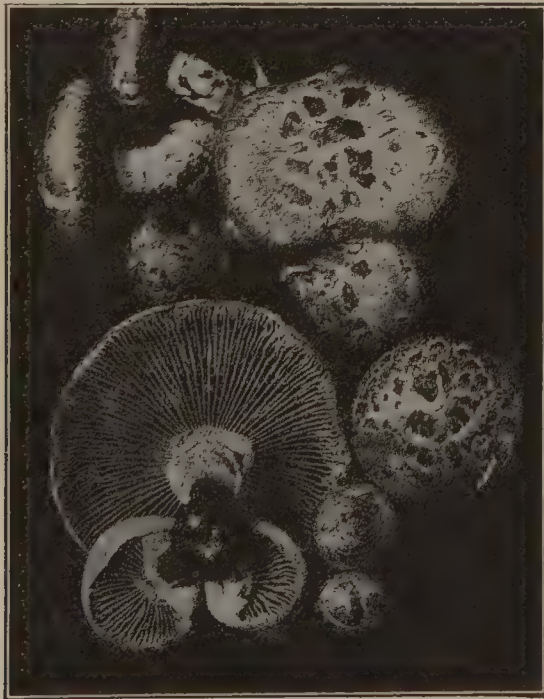


FIG. 301.—*Lentinus lepideus*. After Hard.

L. conchatus (Bul.) Schr. is found on birch, poplar, aspen.
L. lepideus Fr. on pine, birch, etc.

Marasmius Fries (p. 319)

Sporophore tough, withering, often reviving in renewed moisture; pileus, with few exceptions, regular, thin, leathery, without a veil, sharply differentiated from the stipe, rarely sessile or laterally attached; stipe tough, cartilaginous or horny, without an annulus; gills tough, thin, leathery or membranous, entire margined.

Some four hundred fifty species of wide distribution, but chiefly small tropical fungi.

M. plicatus Wak.

Pileus submembranous, convex or subcampanulate, glabrous, sulcate-striate, chestnut or light wine-colored; gills rather distant, white, basally attached; stipe slender, glabrous above, white, downy below.

This fungus which exists first as a saprophyte resides primarily in the soil from which it grows over the stools of sugar-cane and eventually penetrates living tissue, destroys many roots and smothers the developing buds. The white mycelium is found cementing the lower leaf sheaths to the cane. It is probable that several species are concerned.

Agariceæ (p. 318)

This tribe contains all the gill fungi and is characterized by a fleshy, putrescent sporophore; gills fleshy, rarely tough or leathery, weak, easily broken, not deliquescent, without milky juice. It is the largest tribe of the family. The genera are conveniently grouped as black, brown, rusty, pink or red, and white-spored forms. None of the black-spored species are known as parasites.

Phæosporeæ (Rusty-spored series)

Annulus continuous; veil single, forming the
 annulus.....

1. **Pholiota**, p. 323.

Rhodosporeæ (Pink-spored series)

Stipe central; volva present, annulus wanting
 Volva and annulus both wanting; gills free
 from the stipe.....

2. **Volvaria**, p. 323.

3. **Pluteus**, p. 324.



FIG. 302.—*Marasmius plicatus*. After Fulton.

Leucosporeæ (White-spored series)

- Stipe lateral, or none..... 4. *Pleurotus*, p. 324.
- Stipe central
 - Volva absent; annulus present; gills united to the stipe; pileus usually smooth . . . 5. *Armillaria*, p. 326.
 - Volva and annulus both absent
 - Gills decurrent on the stipe; stipe fleshy. 6. *Clitocybe*, p. 327.
 - Gills adnate, stipe with a cartilaginous rind..... 7. *Collybia*, p. 328.
 - Gills sinuate; stipe with a cartilaginous rind; pileus membranous, more or less striate..... 8. *Mycena*, p. 329.

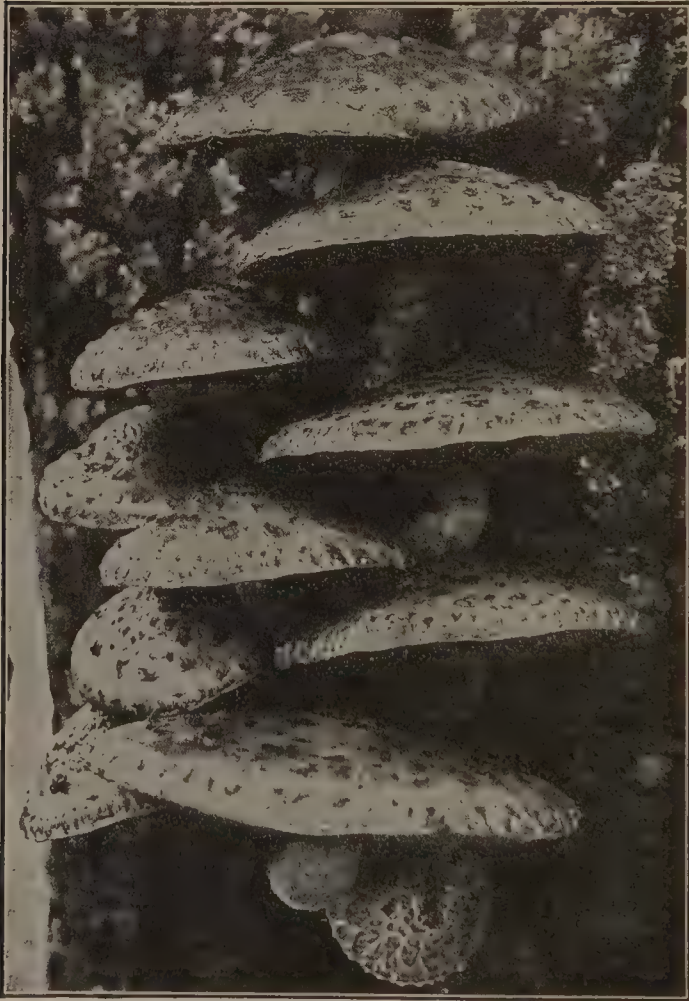


FIG. 303.—*Pholiota adiposa*. After Freeman.

Pholiota Fries (p. 320)

Pileus symmetrical, more or less thick, fleshy, with a veil which forms an annulus; gills adnate, becoming rusty at maturity. Fig. 303.

P. aurivilla (Bat.) Quel. and **P. squarrosa** Müll. occur on deciduous trees, especially on the apple.

P. spectabilis Fr. is occasionally parasitic on oaks.

P. mutabilis (Schä.) Quel. is a root parasite on trees.

P. adiposa Fries.

Cap medium, 5–10 cm. wide, yellow, very sticky when moist, with spreading or erect, rust-brown scales which sometimes disappear when old, convex to plane; stem 5–15 x 1–2 cm., yellow, paler above and darker, scaly below the more or less imperfect tufted ring, solid or stuffed; gills adnate, yellowish to rust-colored, broad, crowded; spores rust-colored, elliptic, 7–8 x 5 μ . The name may refer to the sticky cap.

Chiefly a saprophyte, occasionally on living trees, both deciduous trees and conifers, as a wound parasite.

P. destruens Broud. occurs on poplar;

P. cervinus Schä. on various trees.

Volvaria Fries (p. 320)

Fleshy, gills free, white, later pink; spores ellipsoid, smooth; annulus none; volva present. Easily distinguished from all other pink-spored genera by the volva. Fig. 304.

About thirty-six species.

V. bombycina (Schä.) Quel.

Cap large, 8–25 cm. wide, all white and silky, more rarely somewhat scaly, hemispheric or bell-shaped to convex; stem 8–12 x 1–2 cm., white, smooth, tapering upward, solid, volva large and spreading; gills free, salmon-pink, crowded, spores elliptic, 6–7 x 4 μ . It is often parasitic on various trees.



FIG. 304.—*Volvaria bombycina*.
After Atkinson.

Pluteus Fries (p. 320)

Pileus fleshy, regular, separating easily from the stipe; gills free; volva and annulus both absent; spores elliptic.

P. cervinus Schä. Fig. 305.

Cap large, 5–16 cm. wide, usually some shade of brown, from grayish or yellowish to blackish-brown, more or less fibrous or hairy on the disk, sometimes sticky, convex or plane; stem 7–15



FIG. 305.—*Pluteus cervinus*. After Atkinson.

x $\frac{1}{2}$ –1 cm., brownish, smooth or black-hairy, solid; gills free, pink, broad; spores pink, rarely greenish, globose, 7–8 x 5–6 μ .

A common saprophyte which is occasionally parasitic.

Pleurotus Fries (p. 322)

Pileus laterally sessile or excentrically stipitate. Fig. 306.

A genus of about two hundred fifty species.

P. ostreatus Jacq.

Cap large, 7–24 cm. wide, white, gray or tan, smooth or more or less scaly in age, convex or plane, shelf or shell-shaped, more or less lobed and torn at the margin; stem short and lateral, or none, white, solid, more or less hairy at base; gills long-decurrent, connected by veins on the stem, white or yellowish; spores elliptic, 8–10 x 4–5 μ .

Common on deciduous trees, mainly saprophytic.

P. salignus Schräd. is often parasitic on willow, poplar, mulberry, etc.

P. ulmarius Bul.

Cap large, 8–15 cm. wide, white, whitish or tan, often brownish toward the center, smooth, often cracked, usually convex, sometimes plane; stem long and stout, often nearly central, 5–12 cm.

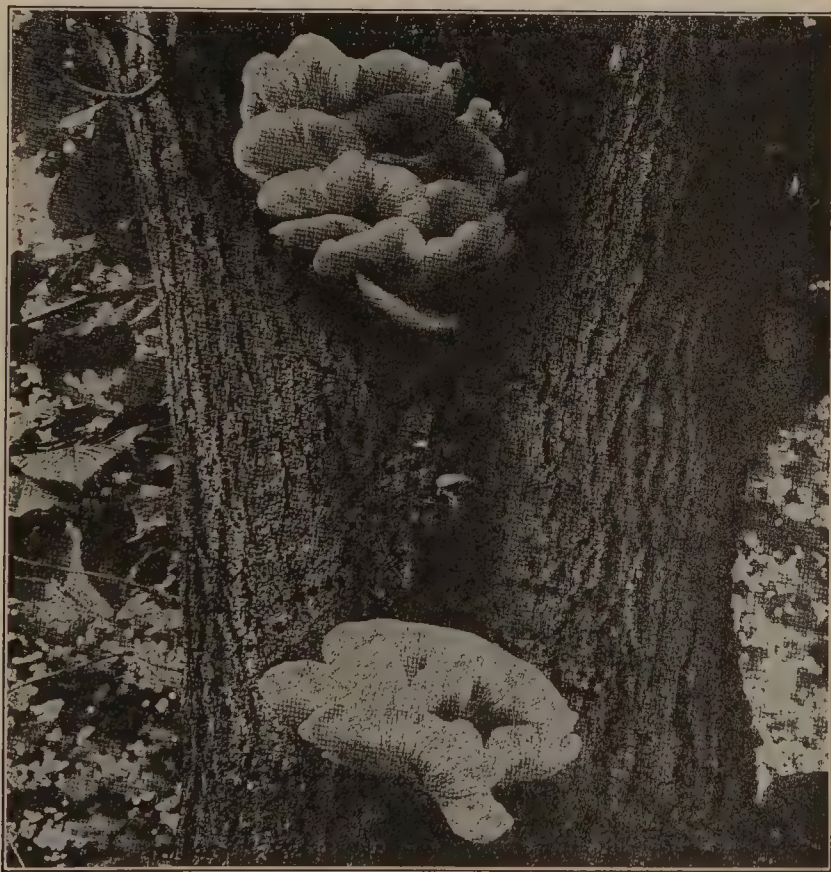


FIG. 306.—*Pleurotus ostreatus*. After Clements.

by 2–3 cm., white or tan, smooth or hairy toward the base, solid, elastic, often curved; gills annexed or sinuate, whitish, broad, close; spores globose, 5–6 μ .

Parasitic on elm and maple or usually a saprophyte.

Other questionable parasites are: *P. atrocæruleus* Fr. on willow; *P. mitis* Pers. on pine; *P. corticatus* Fr. on poplar.

Armillaria Fries (p. 322)

Fleshy, the substance of the pileus and stipe continuous; annulus fixed; gills usually attached, white; spores clavate, ellipsoid or ovate, smooth.

About sixty species. Fig. 308.

A. mellea (Vahl) Quel.

Cap large, 3–15 cm. wide, usually honey-colored, but varying through all shades of yellow to brown, typically marked with small tufts of brownish or blackish hairs, especially toward the center, though sometimes woolly or entirely smooth, margin often striate, convex to expanded; stem tall, stout, 3–15 cm. by 6–20 mm., whitish, yellowish, or brownish, especially below the ring; smooth or scaly, hollow or stuffed, ring usually thickish and conspicuous, but sometimes thin or even lacking; gills touching broadly or running down the stem, whitish or yellowish; spores elliptic or rounded, 7–10 μ .



FIG. 307.—Rhizomorphs of *A. mellea*.
After Freeman.

This is a common wound parasite of conifers and deciduous trees, causing a root-rot, especially important on apple, peach,

cherry, plum, also on *Rubus*. It is also reported as the cause of a potato root-rot. The abundant mycelium is white and extends a meter or more through the wood and bark, aggregating under or on the bark to form shining, hard, gray-black, intertangled cords, rhizomorphs, 1–2 mm. in diameter often reaching out to great distances through the earth. Fig. 307. Sheets of white felt also occur.

The young mycelium grows into the cambium layer, attacking living cells and often encircling the tree. In the living cortex it presents a characteristic fasciated skin-like appearance.

The sporophores are borne in clusters in autumn on the ground or on the bark.

The spores, sown in plum decoction, develop a mycelium which soon produces rhizomorphs. These advancing give off delicate hyphæ which may penetrate into the host. The mycelium spreads



FIG. 308.—*Armillaria mellea*. After Wilcox.

most rapidly through the medullary rays and from them into other tissue elements.

A. mucida (Schräd.) Quel. is reported as a wound parasite of the beech.

Clitocybe Fries (p. 322)

Pileus more or less fleshy, margin at first incurved; stipe fleshy, often becoming hollow; gills decurrent.

About ninety species.

C. monadelphæ Morg. = *C. parasitica* Wil.

Growing in dense clusters; pileus 6–8 cm., convex or umbonate,

usually minutely scaly, mottled buff to yellow-brown in color; gills paler, becoming mottled, at first noticeably decurrent; stipe 10–16 cm. thick, solid, usually curved, darker than the pileus; black rhizomorphs present.

It differs from *Armillaria mellea* in having no annulus, and in growing in denser clusters.

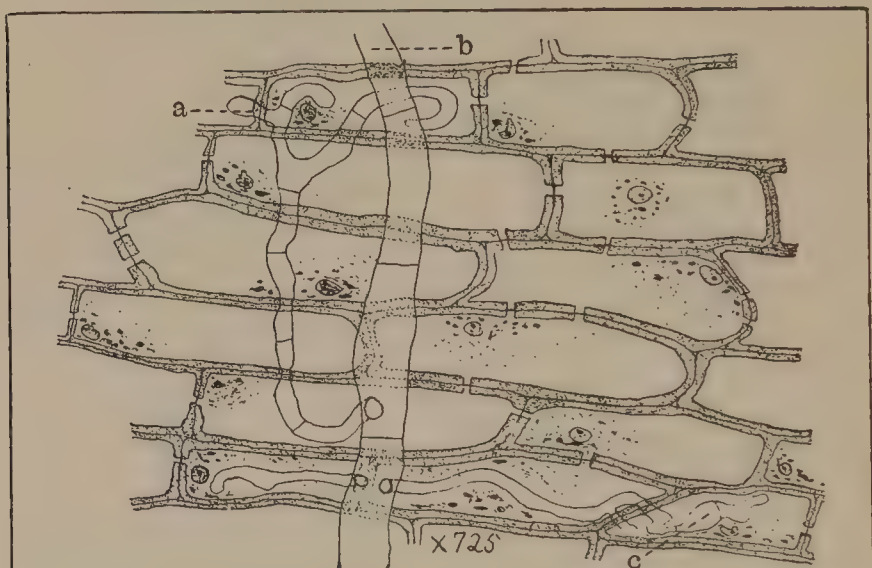


FIG. 309.—*Clitocybe monadelphae*, mycelium entering medullary ray. After Wilcox.

The fungus causes a root-rot of apple very similar to that caused by *Armillaria mellea*. There are present typical subcortical strands, mostly between the cortex and cambium, and sometimes characteristic subterranean black rhizomorphs adhering close to the cortex of the roots.

Fungous branches enter the wood chiefly through the medullary rays and there is later rapid vertical growth through the vessels and tracheids. The cell contents are destroyed, the hyphæ often forming loops around the nucleus. The sporophores occur in groups at the base of the tree after the disease is well developed.

***Collybia* Fries (p. 322)**

Pileus thin, fleshy, margin at first incurved; stipe cartilaginous. About two hundred seventy-five species. Fig. 310.

C. velutipes Curt.

Cap 2-8 cm. wide, yellow-brown or reddish brown, rarely paler except toward the margin, smooth, very sticky when moist, convex to plane or somewhat recurved, often excentric or irregular through pressure.

A common saprophyte which is reported by Stewart as the probable cause of death of the horse chestnut, also in linden.



FIG. 310.—*Collybia velutipes*. After Lloyd.

Mycena Fries (p. 322)

Small, pileus usually bell-shaped, rarely umbilicate, membranous and more or less striate, at first with the straight margin applied to the stipe; gills only slightly toothed, not decurrent or only so by a tooth; stipe slender, cartilaginous, usually hollow. Fig. 311.

A genus of some three hundred species.

M. epipterygia Scop.

Five to ten cm. high; pileus 1-2 cm. broad, viscid when moist, ovate to conic or campanulate, later more expanded, obtuse, the margin striate, sometimes minutely toothed, grayish, in age often reddish, stipe 2 mm. thick, flexuous or straight with soft hairs at the base; gills decurrent by a small tooth, varying in color from whitish through gray to a tinge of blue or red.

Usually a saprophyte, but injurious to various kinds of trees. Widely distributed in the North temperate zone.

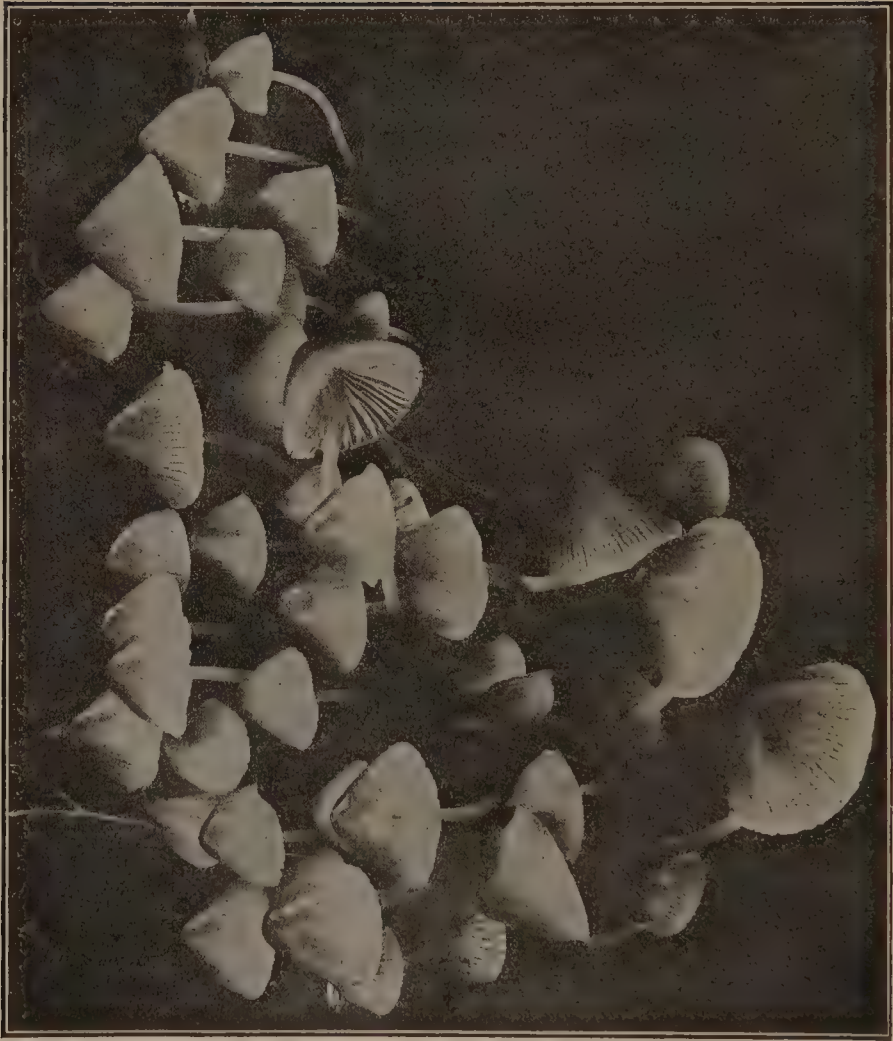


FIG. 311.—*Mycena galericulata*. After Clements.

FUNGI IMPERFECTI ^{1, 2} (p. 56)

In the preceding pages it has been repeatedly evident that one species of fungus may have two, even several different types of spores; in the Erysiphales the perithecial form and the conidial; in the Peronosporales oöspores and conidia; in the Sphæriales the ascigerous form and several conidial forms; in the Basidiomycetes the basidial form and various conidial forms; in the Uredinales spring and summer stages and teliospores. Many of the lower or conidial forms are known while the higher spore forms, ascigerous, basidial, or sexual form, are not known to be genetically connected with them, though it seems very probable, reasoning by analogy, that these conidial forms really constitute part of the life cycle of some fungus which embraces also a higher form of spore. It is probable, indeed certain, that some of these conidial forms at present possess also higher, as yet unknown, forms of fructification. It is likewise probable that in many cases the conidial form, though it does not now possess any higher spore form, did in its not remote phylogeny possess such forms; indeed that all of them are phylogenetically related to fungi which produced one of the higher types of spores.

In some cases even in the absence of the higher spore it is possible to refer the fungus to its proper order as, for example, is the case with the conidial forms of the Peronosporales, the summer or spring forms of the Uredinales, or the Oidium forms of the Erysiphaceæ.

Regarding many thousands of other conidial forms such reference is impossible or hazardous, since from the conidial form the form of the higher spore can be inferred with only a small degree of accuracy or not at all. For example, the conidial form known as *Glæosporium* in the higher form of some of its species proves to be a *Glomerella*, in other cases a *Pesudopeziza*; some *Fusariums* prove to belong to the life cycle of *Nectria*, others to that of *Neocosmospora*, etc.

In plant pathology and in systematic mycology it becomes necessary to classify, for convenience of reference and designation,

¹ A new system for classification has recently been proposed. v. Höhnelt, *System der Fungi imperfecti* Fuckel. *Mykologische Untersuchungen und Berichte* 1: Part 3, 301, 1923.

² Diedicke, H. *Über die Systematik der Fungi imperfecti*. *Mitt. Thur. Bot. Ver. Weimar*. 31: 71, 1914.

these multitudinous conidial forms of which the higher spore form is as yet unknown, which may exist now or which may have existed only in the more or less remote past. From analogy it is probable that most of them pertain to the Ascomycetes, though a few may find place among other classes.

This whole group of forms, which is characterized chiefly by the imperfection of our knowledge of them, is classed together under the name **Fungi Imperfecti**.

The Fungi Imperfecti are in a temporary way divided into orders, families, genera and species as are other fungi, with full recognition of the fact that future research will result, in many cases, in the disclosure of higher spore forms and the consequent removal of species to their proper place in the general scheme of classification.

Recognizing the tentative nature of the genera in the Fungi Imperfecti these are spoken of as "form-genera."

Pathologically, the Fungi Imperfecti are of high importance, often occurring on leaves, stems, fruit, wood, bark, etc., as active parasites, though very many are also saprophytes. Upon leaves they are particularly common causing diseased areas known as "leaf spots."

The Fungi Imperfecti display three principal types of fructification, **pycnidia**, **acervuli** and **hyphæ**.

Pycnidia are more or less spherical, hollow sporocarps on the inside of which conidia are borne on stalks, **conidiophores**, arising from the base or base and sides. Figs. 314, 325. The pycnidium may be of various colors though it is most commonly black or dark; it may be superficial or imbedded, and with or without a beak, **rostrum**. The opening for the escape of the spores, **ostiole**, may be narrow or wanting, or it may be very large, round, irregular, etc. The walls vary from extremely delicate to very thick, smooth or variously provided with hairs, spines, etc.

As need arises, it is common to speak of micro-pycnidia, and macro-pycnidia. Pycnidia with very small spores are sometimes called spermogonia, especially if the spores do not germinate, a custom to be deprecated.

The **acervulus** may be regarded as a pycnidium without its wall. It consists of a close bed of short conidiophores. Figs. 337, 339. Acervuli may be small or large, subepidermal, subcortical or superficial and may or may not be provided with hairs (**setæ**) Fig. 337, of various kinds. An acervulus with a well marked basal stroma

is known as a **sporodochium**. Fig. 393. If the sporodochium stalk is markedly developed the structure becomes a **coremium**. It is sometimes quite difficult to distinguish between a pycnidium with an extremely large ostiole, or one with a very thin wall, and the acervulus. For such purposes thin longitudinal sections are most useful.

Hyphæ are conidiophores which grow for some distance above their supporting substratum and in more loose form than in the acervuli, so that the terminal parts at least stand out as separate threads, Figs. 346, 351, 361, 363.

The hyphæ may be simple and short, or long and much branched. When the hyphæ are very short and closely crowded to form a sporogenous cushion the condition of an acervulus is approached and confusion arises.

The **conidia** borne in the pycnidia, acervuli or on the hyphæ are of as various forms and types as is well conceivable and are made the chief basis for subdivision of orders into form-genera. They may be simple or compound, of almost any color, and may be borne in bisipetal succession in chains, or solitary, or in groups at the apices of the conidiophores.

The following scheme of Saccardo presents the confessedly artificial groups into which conidia may for convenience be divided.

SCHEME OF SPORE SECTIONS

Amerosporæ: spores 1-celled, not stellate, spiral or filiform

Hyalosporæ: spores hyaline or clear, globose to oblong, continuous

Phæosporæ: spores dark, yellow to black, globose to oblong, continuous

Didymosporæ: spores, 2-celled

Hyalodidymæ: spores hyaline, 2-celled

Phæodidymæ: spores dark, 2-celled

Phragmosporæ: spores 3 to many celled by cross septa

Hyalophragmiæ: spores hyaline, 3 to many-celled

Phæophragmiæ: spores dark, 3 to many-celled

Dictyosporæ: spores septate, both crosswise and lengthwise, i. e., muriform

Hyalodictyæ: spores hyaline, muriform

Phæodictyæ: spores dark, muriform

Scolecosporeæ: spores needle-shaped to filiform, continuous or septate

Helicosporæ: spores spirally twisted, hyaline or dark, continuous or septate

Staurosporæ: spores stellate or radiate, hyaline or dark, continuous or septate

The mode of bearing spores and the color of the fungus both of which it is seen are made the basis of classification have been shown by Stevens and Hall and others to depend largely on environment, while the septation of the spores, also a fundamental character in present classification, depends often on the age of the spores or on other factors. Many spores are unicellular until germination begins but then become typically 2-celled; e. g., *Gloeosporium*. Such conditions have led to much inaccuracy in description and doubtless to undue multiplication of form-species.

It has been quite customary, excusably so, to describe as new a form-species when no form-species previously described for the same host or its near botanical kin could be regarded as identical with it. Thus a *Septoria* found on *Vitis* would ordinarily be regarded as new unless some of the *Septorias* already described on some of the *Vitaceæ* seemed to be the same, even though indistinguishable from dozens of *Septorias* on other families of plants. This course has led to enormous multiplication of so-called species in these form-genera giving rise to such form-genera as *Septoria*, *Cercospora*, *Phoma* and *Phyllosticta* with species numbering more than 1200, 700, 1600, 1200, respectively.

Many of the form-genera are purely artificial—not at all well founded, e. g., *Phoma* is separated from *Phyllosticta* only by the supposed inability of the latter to grow on structures other than leaves, a distinction which has been shown to be quite untenable. It is evident that much careful study by cultures and cross inoculations is needed to reveal the true status in these fungi.

Since the conception of species is here most loose the form species given below must be regarded as purely tentative. The names are to serve merely as handles for convenience in treating of the various parasites and in only comparatively few instances do they signify that they are really species. In many cases forms appearing under two or more names may prove eventually to be identical while in other cases forms may need to be subdivided.

KEY TO ORDERS OF Fungi Imperfecti

- | | |
|---|--------------------------------------|
| Conidia produced in pycnidia..... | 1. Sphærospidales , p. 335. |
| Conidia not in pycnidia | |
| Hyphæ innate within the matrix.... | 2. Melanconiales , p. 364. |
| Hyphæ somewhat superficial, often
floccose..... | 3. Moniliales , p. 377. |
| Conidia or other special reproductive
cells unknown..... | 4. Mycelia sterilia , p. 435. |

The Sphæropsidales (p. 334)

Conidia in pycnidia which open by pores or slits, superficially resembling the perithecia of the Ascomycetes.

The Sphæropsidales are preëminently leaf-spotting fungi though many of them grow on fruit or stems causing blight, rot, cankers etc. The vast majority are saprophytes or parasitic on tissues of weak vitality, but not a few are active parasites.

KEY TO FAMILIES OF Sphæropsidales

Pycnidia globose, conic, or lenticular

Pycnidia membranous, carbonous or coriaceous, black.....

1. **Sphærioidaceæ**, p. 335.

Pycnidia more or less dimidiate, irregular or shield-shaped, black.....

2. **Leptostromataceæ**, p. 360.

Pycnidia cup-shaped or patelliform, black.....

3. **Excipulaceæ**, p. 363.

The Sphærioidaceæ¹

Pycnidia globose, ovate, or clavate, leathery to carbonous, black or dark brown, opening by a pore, superficial, erumpent or covered; stroma present or absent; conidia variable in form, color, and division.

The family is subdivided according to its spores as indicated on p. 333.

Sphærioidaceæ-Hyalosporæ

Spores hyaline, 1-celled, spherical, elliptical or long.

KEY TO GENERA OF Sphærioidaceæ-Hyalosporæ

Stroma none; pycnidia separate

Pycnidia smooth; conidia borne singly, unappendaged

Pycnidia free in the substratum; subiculum none

Pycnidia not beaked

Pycnidia opening by a regular pore, more or less sunken in the substratum

Conidiophores simple or nearly so; pycnidia at first covered, then erumpent

Spores under 15 μ

On leaves only..... 1. **Phyllosticta**, p. 336.

¹ Diedicke, H. Sphæropsidæ. Ann Myc. 9: 279, 1911.

- Not on leaves..... 2. *Phoma*, p. 340.
- Spores over 15 μ 3. *Macrophoma*, p. 343.
- Conidiophores branched..... 4. *Dendrophoma*, p. 344.
- Pycnidia opening irregularly;
spores blunt..... 5. *Plenodomus*, p. 344.
- Pycnidia beaked..... 6. *Sphæronema*, p. 345.
- Pycnidia on a radiate subiculum... 7. *Asteroma*, p. 346.
- Pycnidia appendaged or hairy with long
bristles, usually covering the entire
pycnidium, conidia cylindric fusoid,
usually curved..... 8. *Vermicularia*, p. 346.
- Pycnidia stromatic, superficial or sunken
 - Pycnidia single on the stroma
 - Pycnidia with a single chamber
 - Conidiophores filiform; conidia of
two kinds..... 9. *Phomopsis*, p. 342.
 - Conidiophores indistinct or absent;
stroma indistinct..... 5. *Plenodomus*, p. 344.
 - Pycnidia several on each valsooid stroma
scattered irregularly; conidia sepa-
rate from each other
 - Conidia straight, large, fusiform..... 10. *Fusicoccum*, p. 346.
 - Conidia, ovate, or elongate
 - Pycnidia superficial or subsuper-
ficial; conidiophores simple. 11. *Dothiorella*, p. 347.
 - Conidia allantoid..... 12. *Cytospora*, p. 348.

Phyllosticta Persoon^{1, 2, 3} (p. 335)

Pycnidia immersed, erumpent or with the beak piercing the epidermis, lenticular to globose, thin membranous, opening by a pore; conidia small, ovate to elongate, continuous, hyaline or green; conidiophore short or almost obsolete. On leaves.

In part = *Guignardia*, *Valsonectria*, *Mycosphaerella*.

The genus is a very large one of over twelve hundred forms, few of which have been adequately studied. It differs from *Phoma* only in that it is foliicolous while *Phoma* is caulicolous, a distinction which is not consistently maintained and which is untenable for generic limitation (see p. 334).

The fungus produces leaf spots by killing or weakening the

¹ Seaver, F. J. *Phyllostictales*. North American Flora. 6: pt. 1, 1922.

² Ellis, J. B. and Everhart, B. M. The North American *Phyllostictas*. 1900.

³ Anderson, P. J. Index to American species of *Phyllosticta*. Mycol. II, 66, 1919.

leaf tissue with its mycelium. The spots are circular or subcircular, unless rendered angular by obstruction by veins, and the pycnidia may usually be seen with a lens in old spots unless the color of the leaf forbids. Similar effects follow on fruits.

P. bellunensis Mart. on elm = *Mycosphærella ulmi*.

P. brassicæ (Curr.) West. on cabbage, etc. = *Mycosphærella brassicæcola*.

P. sphæropsidea E. & E. = *P. paviæ* Desm. = *Guignardia aesculi*, see p. 170.

P. labruscæ Thüm. on the grape = *Guignardia bidwellii*. See p. 166.

P. tabifica Prill. is perhaps identical with *Mycosphærella tabifica*, See p. 175.

P. maculiformis (Pers.) Sacc. on chestnut = *Mycosphærella maculiformis*.

P. solitaria E. & E.

Pycnidia globose or sub-globose developing subepidermally; on the leaves 60–120 μ high, 60–110 μ wide, on the fruit and bark 60–95 μ high x 107–166 μ wide and usually with distinct ostioles which are rostrate on the fruit and leaves. Spores broadly elliptic and coarsely guttulate, 7–11 x 6–8.5 μ . Pycnosclerotia produced

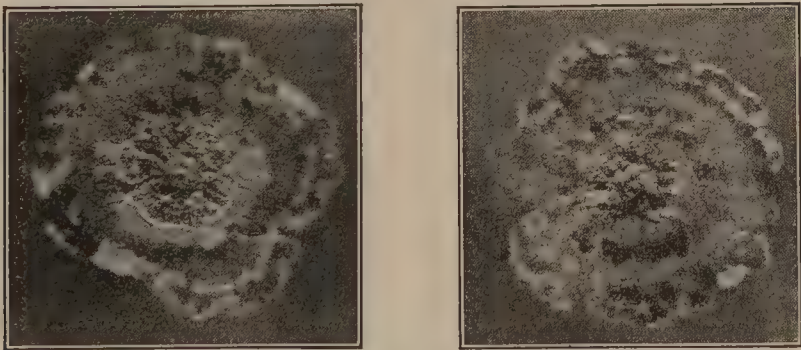


FIG. 312.—*P. solitaria*. 1-month-old colony on apple agar. After Scott and Rorer.

in the autumn, solitary or stromatic, large, 155–274 μ wide, 107–238 μ high with thick, dothideaceous membranes and without a definite ostiole; pycnosclerotia spores formed from the pseudo-parenchyma context and bearing a gelatinous cap or attenuated appendages at the broad pole. Conidiophores always present, distinct, columnar or filiform. Cells of the mycelium with large globules.

This fungus closely resembles *Phoma uvicola* B. & C., *Phyllosticta paviae* Desm., *P. congesta* Heald and Wolf and the imper-

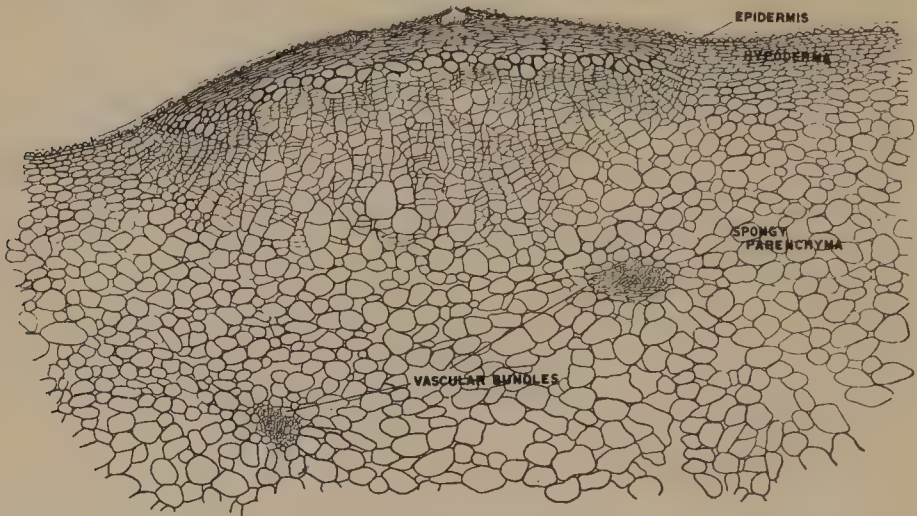


FIG. 313.—*P. solitaria*, section showing the dead tissue near the surface; the absciss layer and the modified tissue below it. After Guba.

fect form of *Guignardia vaccinii* and the ascigerous form, as yet unknown, is probably a *Guignardia*.

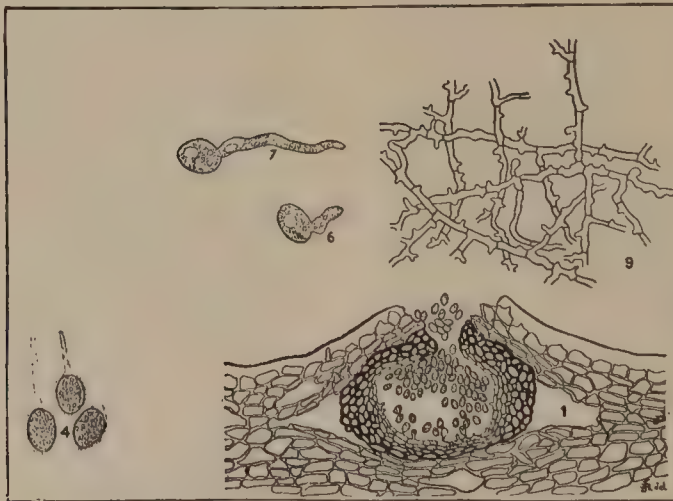


FIG. 314.—*P. solitaria*. 1, section through apple; 4, spores from apple blotch showing appendages; 6-7, germinating spores; 9, mycelium from corn-meal cultures. After Scott and Rorer.

The cause of cankers on the twigs, petioles and pedicels; of leaf spots and of fruit blotches of apple.

P. limitata Pk. is reported on apple but probably is saprophytic.

Spots round, minute, 2–6 mm., brown or reddish; pycnidia epiphyllous, black, few, punctiform; spores ellipsoid, $7-8 \times 4 \mu$.

P. pirina Sacc.

Spots variable; pycnidia epiphyllous, punctiform, lenticular, $100-130 \mu$, context loosely cellular, brown; conidia ovoid to ellipsoid, $4-5 \times 2-2.5 \mu$.

This was long regarded as the chief factor causing the common leaf spot on the apple and pear. Recent work throws doubt on this.

P. congesta H. & W.

Spot 0.5–0.8 mm., brown, vein-limited; pycnidia solitary, $50-125 \mu$; spores globose or slightly elongate, hyaline, $6-9 \mu$. On plum leaves, fruit and twigs, causing blotch.

P. circumscissa Cke.

Amphigenous; spots orbicular, reddish-brown, at length deciduous; pycnidia scattered, minute; conidia elliptic, $8 \times 2 \mu$.

Spots and shot holes are formed on drupaceous hosts.

P. prunicola Sacc.

Spots subcircular, epiphyllous, sordid-brownish or ochraceous, margin subconcolorous; pycnidia scattered, punctiform; conidia ovoid to ellipsoid, $5 \times 3 \mu$.

It is found on *Prunus*, causing leaf spots. Scurf is also produced on apple bark.

P. betæ Oud.

Spots grayish-ochre, large and irregular; pycnidia epiphyllous, minute, densely clustered, brownish, subimmersed; conidia elliptic, $5-6 \times 3 \mu$.

The cause of leaf spots of beets.

P. chenopodii Sacc.

Spots irregular, scattered or confluent, ochraceous, fuscous margined; pycnidia lenticular, punctiform, 50μ ; conidia oblong-elliptic, $5 \times 3 \mu$. A leaf spot is produced on spinach.

P. apii Hals. forms brown spots on leaves of celery; pycnidia punctiform, black; conidia elliptic to ovate oblong.

P. phaseolina Sacc.

Spots irregularly scattered, subcircular, 2–10 mm., deep rusty brown, becoming lighter in center and darker margined; pycnidia scattered, $70-90 \mu$; conidia ovoid oblong, $4-6 \times 2-2.5 \mu$.

It causes spotting of bean and cowpea.

P. cucurbitacearum Sacc.

Spots epiphyllous or amphigenous, sordid, whitish; pycnidia

punctiform, 80–100 μ , lenticular; conidia oblong, 5–6 x $2\frac{1}{2}$ μ , curved.

On muskmelon, cucumbers and other cucurbits, spotting the leaves.

P. althæina Sacc.

Spots irregular, with a dark brown margin; pycnidia few, lenticular, 90 μ , ochraceous; conidia ovate-oblong, 6–7 x 3–4 μ .

On hollyhock.

P. caryæ Rand. Spots large, irregular, often confluent, at first yellowish, then brown, sometimes becoming grayish in the center; perithecia 100 μ broad, punctate, epiphyllous; spores irregularly elliptical, 5 x 2 μ .

On living leaves of hickory and the cause of nursery blight of Pecan.

P. straminella Bres. is injurious on rhubarb.

Other species are on peach, apple, pear, apricot, Ribes, strawberry, cranberry, olive, hemp, hop, sweet potato, tobacco, alfalfa, rice, Hedera, rose, carnation, primrose, violet, hydrangea, lilac, cyclamen, digitalis, chrysanthemum, calla, vinca, antirrhinum, Pteris, narcissus, anthurium, dracæna, funkia, Laurus, elm, maple, horse chestnut, chestnut, box elder, catalpa, magnolia, ash, oak.

Phoma (Fries) Desmaziere ^{1, 2} (p. 336)

The genus as at present recorded contains over sixteen hundred forms. It is indistinguishable from Phyllosticta (see p. 336) except that it is caulivorous. Several species are regarded as conidial forms of Diaporthe, Mycosphærella, etc.

P. reniformis on grape=Guignardia bidwellii. See p. 166.

P. albicans Rob. & Desm. on chicory=Pleospora albicans.

P. betæ Fr. on beet=Mycosphærella tabifica. See p. 175.

P. bohémica Bub. & Kab. on fir tree needles=Rehmielliopsis.

P. ambigua (Nitz.) Sacc. on pear=Diaporthe ambigua.

P. sarmentella Sacc. on hop=Diaporthe sarmentella.

P. pomi Pass. =Cylindrosporium pomi Brooks.

Pycnidia papillate, 50–115 μ in diameter. Conidiophores short, conidia 2–3.5 x 0.8–1.0 μ . It is reported as common on apples of almost all varieties, causing small, dry, sunken, brown fruit spots.

¹ Höhnelt, F. v. Über die Gattung Phoma. Ann. Myc. **16**: 98, 1918.

² Shear, C. L. Phoma: A Sample of Mycological Nomenclature and Classification. Mycologia **15**: 174, 1923.

P. lingam (Tode) Desm.¹ = *Phoma oleracea* Sacc.

Pycnidia scattered, globose-depressed, 100-400 μ in diameter, subepidermal or superficial, often beaked; spores 3.5-5 x 1.5-2.2 μ , oblong.

On cabbage and several other crucifers.

The pycnidia are sparse on oval, sunken, diseased areas on the

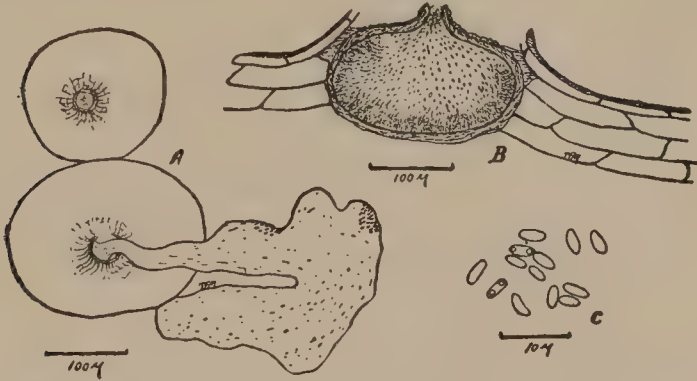


FIG. 315.—*P. lingam*. A, showing pycnidia with spores streaming out; B, section; C, spores. After Manns.

stems, and bacterial invasion follows soon in leaves, cambium, and xylem. In young infections the mycelium is intercellular; when old it penetrates the cells and causes collapse and drying. Infection may occur without wounding, pycnidia following in about two weeks.

P. destructiva Plow., emend. Jamieson.

Spots on tomato fruit, brown to black, membranous or carbonaceous, definite; pycnidia most abundant toward the center of spot, subcutaneous, later erumpent, glabrous, brownish-black, subglobose, slightly papillate, not beaked, ostiolate, 30-350 μ in diameter; conidiophores delicate, filiform, arising from inner cells; spores hyaline, continuous, 1-celled, 3-guttulate, subcylindrical to subglobose, 2.8-8.5 x 1.7-3.4 μ ; produced singly on unbranched filiform conidiophores.

Parasitic on fruit of tomato, spots occurring on green and ripe fruit, usually near the stem end, 1-3 cm. in diameter.

P. apicola Kleb. Causes root rot of celery and occurs also on parsley, parsnip, carrot and caraway.

P. piceina Pk. causes defoliation and death of spruce trees.

¹ Henderson, M. P. The black-leg disease of cabbage caused by *Phoma lingam* (Tode) Desm. *Phytop.* 8: 379, 1918.

Other species are on peach, quince, Citrus, mulberry, grape, wheat and other grains, potato, bean, carrot, mangolds, cotton, sweet potato, hollyhock, lobelia, dahlia, cyclamen, fir, pine, Carpinus.

Phomopsis Saccardo ^{1, 2} (p. 336)

As in *Phoma*, but with both filiform and oval spores.

P. stewartii Pk.

Pycnidia gregarious, commonly occupying grayish or brown spots, thin, subcutaneous, at length erumpent, depressed, minute, $\frac{1}{3}$ – $\frac{1}{2}$ mm. broad, black; stylospores filiform, curved, flexuous or uncinatate, hyaline, $16\text{--}25 \times 1\text{--}1.5 \mu$; spores oblong or subfusiform, hyaline, commonly binucleate, $8\text{--}12 \times 2\text{--}3 \mu$; conidiophores slender, equal to or shorter than the spores.

The fungus with its filiform spores only was noted as a parasite on *Cosmos* by Halsted.

P. mali Roberts

Pycnidia subglobose, scattered, aggregate or in a stroma, black, carbonaceous, plurilocular, ostiolate; spores subfusoid, containing two oil drops, continuous, hyaline, $7\text{--}10 \times 3\text{--}4 \mu$; conidiophores awl-shaped, $20 \times 2.5 \mu$; stylospores thread-like, hooked or S-shape, attenuate, $20\text{--}36 \times 1.5 \mu$.

On leaves and fruit of apple causing spots and on bark causing canker which results in death of the twig or branch.

P. citri Fawcett

Pycnidia scattered, ovoid, parenchymatous, green or dark, $200\text{--}450 \mu$ in diameter, erumpent, thick-walled, top easily broken away leaving spores exposed; ostiole $35\text{--}45 \mu$; spores ovate or fusiform, often flattened on one side, hyaline, often 1–3 guttulate, $5\text{--}9 \times 2.5\text{--}4 \mu$; conidiophores $1.5 \times 12\text{--}15 \mu$; stylospores $20\text{--}30 \times 0.75\text{--}1.5 \mu$, easily detached, often curved at one end. On dead branches and decayed fruit of Citrus causing rot.

P. californica Fawcett

Pycnidia mostly clustered, ovoid to conical, dark colored, $160\text{--}300 \mu$ in diameter, erumpent; ostiole $25\text{--}35 \mu$ in diameter; spores ovate, mostly rounded at both ends, sometimes nearly acute at one end, hyaline, $7.7\text{--}9 \times 3.4\text{--}4 \mu$; conidiophores about 15μ long; stylospores $22 \times 0.3\text{--}1.6 \mu$, curved at one end. This fungus differs

¹ Diedicke, H. Die Gattung *Phomopsis*. Ann. Myc. **9**: 8, 1911.

² Grove, W. B. The British species of *Phomopsis*. Kew Bull. Misc. Inf. **49**, 1917.

distinctly from *Phomopsis citri* Fawcett in mode of growth, color, and principally by forming paraphyses instead of spores in culture. On dead outer bark and in decaying fruits of *Citrus*.

P. vexans (Sacc. & Syd.) Harter., = *Phoma solani* Hals., = *Phoma vexans* Sacc. & Syd., = *Ascochyta hortorum* (Speg.) C.O. Sm.

Pycnidia loosely gregarious; on fruit compact, at first buried, later erumpent, black without, beaked, flattened or irregular; on

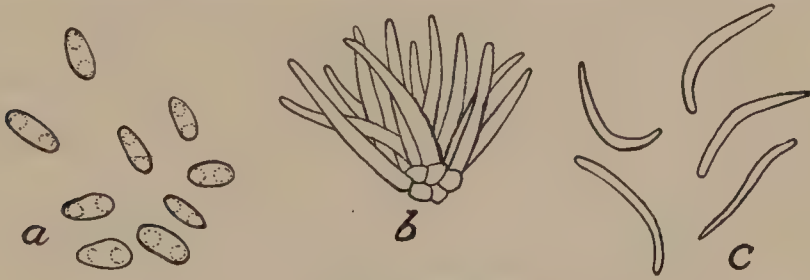


FIG. 316.—*Phomopsis*.

leaves and stems 60 to 200 μ broad, on fruit 120 to 350 μ broad; spores subcylindrical, somewhat acute, 5–8 x 2.8 μ , continuous, hyaline, 2-guttulate, rarely 3; conidiophores simple, short, hyaline, continuous; stylospores filiform, curved, rarely straight, 13–28 μ long.

On leaf stem and fruit of egg-plant, causing stem blight, leaf spot, and fruit rot; also causing damping-off of seedlings.

P. kalmiae Enlows causes a leaf blight of *Kalmia*.

Macrophoma Berlese & Voglino (p. 336)

As in *Phoma*, but the ostiole of the pycnidium not papillate and the pore smaller; conidia over 15 μ long; conidiophores simple, short or filiform.

M. tumefaciens Shear.¹

Pycnidia numerous, depressed, globose, buried in the cortex, subcarbonous, slightly erumpent, subepidermal, 120–350 μ in diameter; ostiole slightly elevated, non-papillate; pore small, dark-colored; pycnosporos elongate, subellipsoid to subrhomboid, mostly obtuse, hyaline to pale lemon-yellow, 24–40 x 7.5–12 μ , ejected in coiled thread-like masses, contents granular; conidiophores 6–12 μ long, simple, filamentous; hyphae dark brown, septate, 10–12 μ wide.

On gall-like swellings of branches and twigs of Poplar.

¹ Hubert, Ernest E. A new *Macrophoma* on galls of *Populus trichocarpa*. *Phytop* 5: 182, 1915.

M. fici Alm. & S. Cam. causes a canker on fig. The pycnidia vary from 150 to 300 μ in diameter; the spores 14–26 x 9–11 μ .

Others are on olive, yew, fir, cassava, hydrangea, ivy, poplar.

Dendrophoma Saccardo (p. 336)

Pycnidia superficial or subepidermal and erumpent, carbonous, ostiole papillate; conidia elongate, conidiophores branched.

A genus of some fifty species, chiefly saprophytes.

D. obscurans (E. & E.) And.¹ Spots large, 0.5–3 cm. or more, circular, oval, or sometimes fan-shaped, brown with broad purple zone; pycnidia scattered, amphigenous, flask-shaped, 150–300 μ , erumpent; spores hyaline, continuous, bacillar or narrowly ellipsoidal, biguttulate, 5–7 x 1.5–2 μ ; conidiophores long, branched. On strawberry causing large leaf spots.

D. marconii Cav. occurs on hemp stems; **D. convallariae** Cav. on leaves of *Convallaria majalis*; **D. valsispora** Penz. on living lemon leaves.

Plenodomus Preuss² (p. 336)

Pycnidia horny, immersed, opening irregularly; spores 1-celled, oblong, hyaline.

P. destruens Harter³

Pycnidia loosely gregarious, at first buried, later erumpent, largest diameter about 300 μ , beaked; conidiophores simple, hyaline fragile, somewhat inconspicuous, 6–13 μ long; conidia oblong, sometimes oval, with rounded ends, 7–10 x 3–4 μ , hyaline, continuous, occasionally slightly curved, 2-guttulate; stylospores 6–15 μ long in the same pycnidium. On the stems of sweet potato.

The organism attacks the cortex of the stem near the ground; also causes rot of the roots.

P. fuscomaculans (Sacc.) Coons⁴

Pycnidia 200–470 μ in diameter, globose, grouped, more or less immersed; spores oblong, 5 x 1 μ , dilute olivaceous.

The cause of a bark canker on apple.

¹ Anderson, H. W. *Dendrophoma* leaf blight of strawberry. Ill. Agr. Exp. Sta. Bul. 229. 1920.

² Diedicke, H. Die Gattung *Plenodomus* Preuss, Ann. Myc. **9**: 137, 1911.

³ Harter, L. L. The foot rot of sweet potato. Jour. Agr. Res. **1**: 251, 1913.

⁴ Coons, G. H. Factors involved in the growth and the pycnidium formation of *Plenodomus fuscomaculans*. Jour. Agr. Res. **5**: 713, 1916.

Sphæronema Fries (p. 336)

Pycnidia superficial or not, pyriform, cylindric or globose, rostrum long; conidia ovate or elongate.

Some seventy-five species, chiefly saprophytes, have been described.

S. phacidioides Desm. on clover=*Pseudopeziza trifolii*. See p. 111.

S. fimbriatum (E. & H.) Sacc.

Pycnidia globose, 100–200 μ , surrounded by septate, hyaline hyphæ; rostrum, 20–30 μ long, apically fimbriate; conidia globose-elliptic, 5–9 μ .¹

The fungus grows in the sweet potato producing dark, almost black spots in the skin. The tissue below becomes olive-green. The dark mycelium is found penetrating through and between cells of the diseased area where numerous olivaceous conidia are also present. The elongated beaks of the pycnidia rise like a small forest from the surface of the potato.

In artificial culture the mycelium is dark, abundantly septate and with numerous oil globules. Long multiseptate conidiophores with light colored tips arise from the medium. From these, hyaline conidia are produced, apparently endogenously. Fig. 317. Olivaceous, globose to elliptical, Fig. 317, conidia are formed within the medium on branches of the mycelium in much the same manner. The pycnidia develop in about nine days after inoculation and the conidia are extruded from the fimbriate mouth of the long rostrum.

Inoculations proved the pathogenicity of the organism, typical black rot appearing in about three weeks after infection.

Other species are on sugar-cane, cranberry, *Prunus*, rice.

¹ Recently Elliott indicated that the spores described as pycnidiospores are really ascospores. (*Phytop.* **13**: 56, 1923).



FIG. 317.—*S. fimbriatum*; 1, pycnidium sending forth spores; 2, hyaline conidia; 6, olive conidia. After Halsted and Fairchild.

Asteroma De Candolle¹ (p. 336)

Pycnidia very small, globose, erumpent, often on a mass of hyphæ; conidia ovate or short cylindric. In part=*Gnomonia*. See p. 196.

A. padi (DC.) Grev. on *Prunus*=*Gnomonia* *padicola*.

Vermicularia Fries (p. 336)

Pycnidia superficial, or erumpent, globose depressed to globose clavate, leathery or carbonous, black, ostiolate or not, beset with rather long, stiff, septate, dark colored bristles; conidia cylindric-fusoid, often curved.

V. dematium (Pers.) Fr.

Pycnidia erumpent, superficial, 80–120 μ , conic, then depressed, often confluent, black, spines pale at the ends, 150–200 x 5 μ , conidia cylindric-elongate, 20 x 4–6 μ , apically rounded, curved.

Commonly a saprophyte, this fungus occasionally causes asparagus disease. On ginseng it produces a stem anthracnose.

Other species are on blue grass, ivy, camellia, carnation, *Sedum*, *Dracæna*, rhubarb.

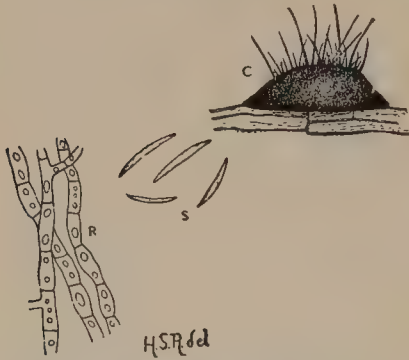


FIG. 318.—*V. dematium*. C, a nearly mature "perithecium"; S, spores; R, hyphæ. After Reed.

Fusicoccum Corda (p. 336)

Stroma subepidermal, several-chambered, erumpent, leathery, black; conidia fusoid, straight and usually large.

Some forty species, several of which are regarded as conidial forms of *Diaporthe* and *Gnomonia*.

F. veronense Massal on Sycamore and Oak=*Gnomonia* *veneta*. See p. 196.

F. viticolum Red. on grape=*Cryptosporella* *viticola*. See p. 203.

F. putrefaciens Sh. is on cranberry.

¹ Diedicke, H. Die Gattung *Asteroma*. *Ann. Myc.* **9**: 534, 1911.



FIG. 319.—*F. viticolum*, compound pycnidium, germinating spores, paraphyses. After Reddick.

Dothiorella Saccardo (p. 336)

Pycnidia erumpent, on a stroma, leathery, ostiole papillate or not; conidia ovate or elongate.

D. ribis (Fcl.) Sacc., on a wide range of hosts = *Diaporthe strumella*.

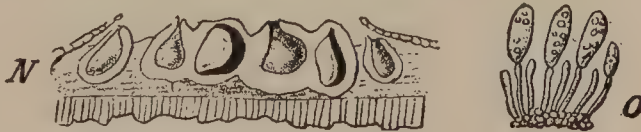


FIG. 320.—*D. mori*. *N*, section of stroma, *O*, conidiophores and conidia. After Allescher.

D. gregaria Sacc.

Pycnidia erumpent, 180–260 μ in diameter; spores oblong-fusoid, hyaline, continuous, spindle-shaped, 18–29 x 5–7 μ ; conidiophores 10–15 x 3–4 μ . The cause of Melaxuma on walnut, in which disease large, black, sunken cankers are produced on limbs and trunk, often accompanied by sudden wilting.

D. quercina (C. & Ell.) Sacc. causes a twig blight of oak.

Cytospora Ehrenberg (p. 336)

Stroma superficial or erumpent, tubercular, with irregular chambers; conidia elongate allantoid. Ascigerous forms belonging to *Valsa* are known.

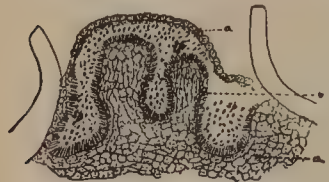


FIG. 321. — *Cytospora*. Section through a stroma. After Chester.

***C. chrysosperma* (Pers.) Fr.¹**

Stromata subcuticular; spores hyaline, allantoid, continuous, $4 \times 1 \mu$, issuing in cirri.

On poplar and willow, chestnut, maple, mulberry, hibiscus, causing canker in trunk, limb and twig.

After the mycelium has grown for weeks in the bark the pycnidia are formed in large numbers.

Sphærioidaceæ-Phæosporæ²

Conidia 1-celled, dark, globose, ovoid or oblong.

KEY TO GENERA OF *Sphærioidaceæ-Phæosporæ*

- | | |
|---|---|
| Conidia large, ovate to elliptic. | 1. <i>Sphæropsis</i> , p. 348. |
| Conidia very small, globose to ellipsoid. . . . | 2. <i>Coniothyrium</i> , p. 349. |

***Sphæropsis* Lévillé**

Pycnidia immersed, erumpent, globoid, black, leathery, membranous, with the ostiole papillate; conidia ovate or elongate; conidiophores rod-like, typically 1-celled, dark.

About two hundred species, several of them important plant pathogens.

S. malorum Pk. = *Physalospora cydoniæ* Arn. See p. 179.

***S. tumefaciens* Hedges**

Perithecia subglobose, papillate, black, ostiolate, erumpent, $152-224 \times 120-192 \mu$; spores oblong or ovoid, continuous or rarely 1-septate, hyaline to pale yellow, $16-32 \times 6-12 \mu$.

The fungus causes tumors, from a few millimeters to 6 cm. in diameter, on lime and orange. These often bear witches' brooms.

¹ Long, W. H. An undescribed canker of poplars and willows caused by *Cytospora chrysosperma*. Jour. Agr. Res. **13**: 331, 1918.

² Diedicke, H. Die braunsporigen sphæropsideen. Ann. Myc. **11**: 44, 1913.

Coniothyrium Corda (p. 348)

Pycnidia subcortical, erumpent or not, globose or depressed, ostiole papillate, black, leathery to carbonous; spores small, ellipsoid, conidiophore reduced or absent.

More than one hundred fifty species.

C. pirinum (Sacc.) Shel. is common on apple leaf spots but is not regarded as their cause.

C. tumefaciens Gus. is described as the cause of a rose canker.

C. fuckelii Sacc. on apple = *Leptosphaeria coniothyrium*. See p. 185.

C. diplodiella (Speg.) Sacc.

Pycnidia minute, subcuticular, erumpent, brown, 100–150 μ ; conidia ovoid to elliptic, 7–11 x 5.5 μ ; conidiophores simple or branched, hyaline, filiform.

This is the cause of a white rot of grapes.



FIG. 322.—*C. diplodiella*, section through pycnidium.
After Scribner.

An ascigerous connection with *Charrina* has been reported in France.

The mycelium is abundant in the affected pulp and sometimes upon the seeds. Peduncles are often killed. The pycnidia are subcuticular, first pink, then white, later brown.

C. caryogenum Rand

Mycelium brown, sometimes almost hyaline where not submerged; pycnidia roundish, ostiolate, thin-walled, dark brown, about 200 x 250 μ in diameter; sporophores short and indistinct; spores pale brownish, elliptical, 1-celled, 2.5–3.6 x 1.8–2 μ .

Upon pecan kernels causing dark-brown, irregularly roundish,

surface spots with a hemisphere of pithy tissue beneath, which is surrounded by a brownish layer of host cells.

Others are on mulberry, elm, vinca.

Sphærioidaceæ-Hyalodidymæ

Conidia hyaline, 1-septate, ovoid, ellipsoid or oblong.

KEY TO GENERA OF Sphærioidaceæ-Hyalodidymæ

Pycnidia separate, not beaked

Pycnidia in discolored areas, maculicole

Pycnidia immersed, then erumpent, perforate; conidia muticate 1. *Ascochyta*, p. 350.

Pycnidia not maculicole, smooth, conidia muticate; conidiophores 1-spored:

Pycnidia without subicle 2. *Diplodina*, p. 351.

Ascochyta Libert¹

Usually producing definite spots; pycnidia globose-lenticular, ostiolate; conidia ovate.

About two hundred fifty species.



FIG. 323.—*A. citri*, spores. After Saccardo.

A. gossypii Syd.² Spots amphigenous, roundish or irregular, 3-10 mm. in diameter, dingy ochraceous, bordered with dark fuscous; pycnidia amphigenous, lens-shaped to globose, 80-100 μ in diameter, ochraceous brown, pierced by a round pore 20-25 μ in diameter; spores oblong or sharply cylindrical, rounded at both ends, 1-septate at or about the middle, not at all or barely constricted, hyaline, 8-10 x 2-4 μ ; sporophores not seen. On cotton leaves, stems, bolls, causing serious injury.

A. ablemoschi Harter³

Spots somewhat circular, often with a brown to black margin, more or less zonate; pycnidia often crowded, brown to black, pyriform to globose, at first buried, becoming erumpent, 65-225 μ in diameter, ostiole small; spores cylindrical to oval, 4-14 x 2-4 μ , hyaline, 1-celled for a long time, finally 1-septate. The cause of a pod spot of okra.

¹ Davis, J. J. North American Ascochytae. Trans. Wis. Acad. Sci. **19**: 655, 1919.

² Elliott, John. A. A new Ascochyta disease of cotton. Ark. Agr. Exp. Sta. Bul. **178**, 1922.

³ Harter, L. L. A hitherto unreported disease of okra. Jour. Agr. Res. **14**: 207, 1918.

A. piniperda Lindau (=Septoria parasitica) is parasitic on fir and spruce causing leaf blight, especially of seedlings.

Pycnidia imbedded in the stem tissue, $85\ \mu$ in diameter; spores 2-celled, ellipsoid, hyaline, $9 \times 1.5\ \mu$.

A. fragariæ Sacc.

Pycnidia partly immersed, black, $100\text{--}125\ \mu$; conidia fusiform to cylindric, constricted, $14\text{--}27 \times 4\text{--}5.5\ \mu$.

This was reported as occurring in injurious form on strawberry leaves, causing spots, at first red, later brown.

A. chrysanthemi Stev.

Pycnidia few, immersed, early erumpent, single or scattered, hemispheric, amber-colored, $100\text{--}200\ \mu$; ostiole central, small, often raised by a neck, dark-bordered; conidia oblong, straight or irregular, $3\text{--}6.2 \times 10\text{--}20\ \mu$, apically obtuse, septum often obscure, sometimes more than one; not constricted till germination.

It causes blighting of ray flowers of chrysanthemums.

A. medicaginis Bres.

Spots small, angular, pale, clustered; pycnidia sublenticular, apiculate, pale, becoming black, $200 \times 160\ \mu$, context parenchymatous; conidia oblong, obtuse, scarcely constricted, $10\text{--}12 \times 4\text{--}4.5\ \mu$. The cause of spots on alfalfa.

A. lycopersici Brum.

Spots red or brown, large, rounded or irregular; pycnidia sparse, minute, black; conidia oblong, constricted, $8\text{--}10 \times 2.5\ \mu$.

Spots are produced on leaves and fruits of egg plant.

Others are on grape, horse-radish, cherry, strawberry, cabbage, beet, lettuce, rhubarb, okra, vetch, tobacco, Melilotus, Polemonium, columbine, pinks, clematis, violet, digitalis, iris, primrose, horse chestnut, maple, poplar, Juglans, ash, spruce, butternut, oak, walnut, and various grasses and grains.

Diplodina Westendorp (p. 350)

Pycnidia immersed or erumpent, globose; ostiole papillate, black, small; spores elongate. It differs from Diplodia only in the hyaline spores.

D. citrullina on cucurbs = *Mycosphærella citrullina*. See p. 174.

Other species are on spruce and willow.

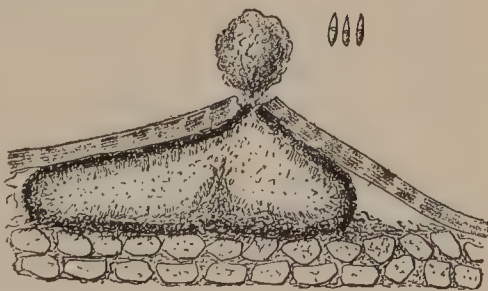


FIG. 324.—*D. castaneæ*, pycnidium and spores.
After Delacroix.

Sphærioidaceæ-Phæodidymæ

Conidia dark, 1-septate, ovoid to oblong.

KEY TO Sphærioidaceæ-Phæodidymæ

- Pycnidia separate, erumpent, not beaked,
smooth; conidia without a mucous
layer, muticate, 15 μ or more long. 1. **Diplodia**, p. 352.
Pycnidia on a subicle enclosed in a hem-
ispheric stroma. 2. **Lasiodiplodia**, p. 353.

Diplodia Fries

Pycnidia immersed, erumpent, carbonous, black, usually ostiolate-papillate; conidia ellipsoid or ovate; conidiophores needle-shaped, simple, hyaline.

Over four hundred fifty species, many of them saprophytes.

D. zeæ (Schw.) Lév.

On ears and stalks of corn, pycnidia borne on the husks, cobs, stalks and rarely the grains, gregarious, small, lenticular to flask-

shaped or irregular, papillate; conidia elliptic, straight or curved, constricted or not, 25-30 x 6 μ .

It occurs as the cause of a very serious dry rot of ear corn.

The growing mycelium is hyaline and much branched.

Pycnidia in the cob are principally on the scales which surround the inner

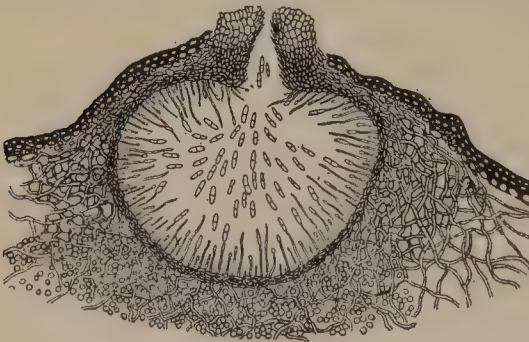


FIG. 325.—Pycnidia of *Diplodia*, from corn kernel.
After Burrill and Barrett.

ends of the kernels and are set in a dense mass of white mycelium. On dead stalks the pycnidia form below the rind, particularly at the nodes, breaking through during the following summer and extruding the spores in cirri.

Spores placed under the husk or in the silk, or sprayed upon plants in suspensions, result in disease.

It is also reported that infection is often by way of the root system, the mycelium reaching the grains through the stem and from the cob.

D. gossypina Cke. causes a rot of the cotton boll and stem.

D. macrospora Earle

Pycnidia scattered, large, erumpent, carbonous; conidia elongate, irregularly clavate, curved or constricted, $70-80 \times 6-8 \mu$.

This is responsible for a corn mold similar to that mentioned above.

D. longispora C. & Ell. causes twig blight of oak and chestnut.

D. natalensis Evans, or a species very near it, is reported as the cause of gummosis of peach and orange in Florida.

Pycnidia scattered, covered, later erumpent, black; papillate, $150-180 \mu$; spores elliptical, 1-septate, not constricted, dark, $24 \times 15 \mu$, exospore with striated bands.

Other parasitic species are on cherries, oranges, avocado, rice, coffee, mulberry, poplar, pine, conifers.

Lasiodiplodia Ellis & Everhart ¹ (p. 352)

Pycnidia collected on a stroma, covered with a brown mycelium, paraphyses among the conidiophores. Otherwise as in *Diplodia*.

L. tubericola E. & E.

Pycnidia globose, $250-305 \mu$; stromatic mass about 1 mm. in diameter; conidia elliptic, $18-22 \times 11-14 \mu$, not constricted; conidiophores short; paraphyses $45-55 \mu$ long, overtopping the conidia.

On sweet potato.

L. trifloræ Higgins

Pycnidia embedded in the cortex, subepidermal or sometimes on the surface of the bark, scattered or aggregated; ostiole not papillate; walls more or less thickened and stromatic, naked or variously covered with hairs; spores oblong, $22-25 \times 13-16 \mu$, at first hyaline and continuous, but becoming dark brown and 2-celled after extrusion from the pycnidia, intermixed with paraphyses.

On trunk and branches of various species of *Prunus* infecting principally the conducting tissue and the medullary rays of the wood and causing gummosis, followed by wilt and death. Entrance is gained through wounds.

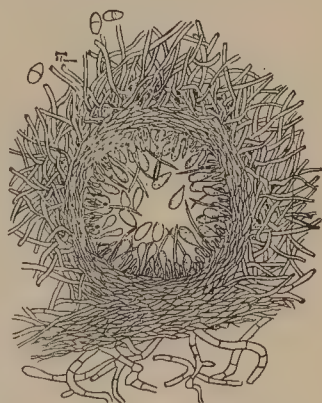


FIG. 326. — *Lasiodiplodia tubericola*. Pycnidium, paraphyses and spores. After Clendenin.

¹ Petch, B. A. On *Lasiodiplodia*. Roy. Bot. Gard. Paradeniya. 4: 445, 1910.

Sphærioidaceæ-Hyalophragmiæ

Conidia hyaline, 2 to many-septate, oblong to fusoid.

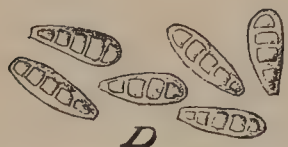
Stagonospora Saccardo

FIG. 327.—*Stagonospora*. *C*, pycnidium in section. *D*, spores. After Corda.

Pycnidia superficial or erumpent, no subicle, globose, ostiolate, papillate, black, membranous or subcarbonous; conidia elongate 3 or more-celled, muticate.

Over one hundred species, chiefly saprophytes; differing from *Hendersonia* only in the hyaline conidia.

***S. carpathica* Bäuml.**

Spots circular, 1–3 mm., light brown with a narrow, darker border; pycnidia 120–180 μ ; conidia escaping in a gelatinous mass, straight or

slightly curved, 14–28 x 4 μ , 2 to 5-celled, frequently slightly constricted. It causes leaf spots on alfalfa.

S. iridis Mass. occurs on iris.

Sphærioidaceæ-Phæophragmiæ

Conidia hyaline, 2 to several-septate, oblong to fusoid.

Hendersonia Berkley

Pycnidia separate, immersed, erumpent or not, globose with a papillate ostiole or depressed, membranous or subcarbonous; no subicle; conidia muticate, elongate or fusoid, 2 to many-septate.

Some two hundred fifty species, chiefly saprophytic, although there are several parasitic species.

***H. mali* Thüm.**

Epiphyllous; pycnidia disciform, large, scattered, black, on brownish, orbicular, violet-margined spots; conidia clavate, apex rounded, base somewhat acute, not constricted, 12–14 x 4–5 μ .

On leaves of apple.

***H. foliicola* (Berk.) Fcl.**

Pycnidia epiphyllous, brownish-black, subglobose, subelliptic



FIG. 328.—*Hendersonia*, hymenium and spores. After Starback.

or irregular; conidia elliptic to clavate, obtuse, 3 to 5-septate; conidiophores filiform, radiating. On *Juniperus* and Pine.

Others are on quince, rice, coffee.

Sphærioidaceæ-Scolecosporæ

Conidia hyaline or light colored, elongate-fusoid, rod-shaped or filiform, continuous or septate.

KEY TO GENERA OF Sphærioidaceæ-Scolecosporæ

- Pycnidia separate, membranous or carbonous,
immersed or erumpent, smooth, not
beaked
Pycnidia maculicole, mainly phyllogenous;
conidia hyaline. 1. **Septoria**, p. 355.
Pycnidia not maculicole
Pycnidia complete at top, usually papil-
late. 2. **Rhabdospora**, p. 359.
Pycnidia more or less incomplete at top,
not exposing a gelatinous mass of
spores, foliicole. 3. **Phleospora**, p. 359.

Septoria Fries^{1, 2, 3}

Pycnidia immersed, usually on leaf spots, globose lenticular, ostiolate, membranous, black; conidia narrowly elongate to filiform, multiseptate, hyaline, conidiophores very short.

Over twelve hundred species, all parasitic, several of them of considerable economic importance but most of them occurring on non-economic hosts.

In part = *Mycosphærella*, *Leptosphæria*.

The genus is a very large one similar to *Phoma* and *Phyllosticta* except in its spore form, and in the ostiole which is frequently very large. *Septoria* and *Phleospora* are distinguished only by the lesser development of the walls of the latter and many species which in early stages pass as *Phleospora* would in older stages be classed as *Septoria*.

Septoria and *Rhabdospora* are distinguished only by the part

¹ Diedicke, H. Die Gattung *Septoria*. Ann. Myc. **10**: 478, 1912.

² Garman, Philip and Stevens, F. L. The Genus *Septoria* presented in tabulation with discussion. Trans. Ill. Acad. Sc. **13**: 176, 1920.

³ Beach, W. S. Biologic specialization in the genus *Septoria*. Amer. Jour. Bot. **6**: 1, 1919.

of the host affected, stem or leaf, and many forms in these two genera are undoubtedly identical.

S. avenæ Fr. = *Leptosphaeria avenaria*. See p. 185.

S. rubi = *Mycosphaerella rubi*. See p. 173.

S. piricola Desm. on pear and apple = *Mycosphaerella sentina*. See p. 173.

S. populi Desm. on *Populus* = *Mycosphaerella populi*.

S. phlogis Sacc. & Speg., on *Phlox* = *Leptosphaeria phlogis*.

S. ribis Desm.

Hypophyllous; spots small, irregular, bounded by the leaf veins, brownish-purple; pycnidia innate, minute, convex, brownish-black; cirri reddish in mass; conidia elongate, linear, curved, $50\ \mu$ long.



FIG. 329.—*S. ribis*, a pycnidium and spores. After Longyear.

On gooseberry and currant, causing leaf spots and defoliation.

S. aciculosa E. & E.

Pycnidia innate to superficial, grouped, minute, amphigenous; conidia needle-shaped, continuous, $15-20 \times 0.75\ \mu$.

It is found on the strawberry.

S. fragariæ Desm.

Epiphyllous; spots suborbicular, brown, with reddish-brown margin; pycnidia minute, innate, prominent, brownish; cirri white; conidia cylindric, obtuse, 3-septate.

Perhaps = *Mycosphaerella fragariæ*. See p. 171.

On strawberry, cultivated and wild, forming circular leaf spots.

S. bataticola Taub.

Pycnidia imbedded under the epidermis, with open mouths protruding or free, varying from $70-130\ \mu$, readily falling out; spores hyaline, vermiform, curved to straight, varying from $15-80 \times \frac{1}{3}-\frac{1}{2}\ \mu$. Parasitic on living leaves of sweet potato.

S. pruni Ellis

Spots dark brown, dry, subrotund, soon breaking out, 1-3 mm.; pycnidia brown, immersed, $60\ \mu$; conidia linear, obtuse, 4 to 6-septate, $30-50 \times 2\ \mu$. On plum.

S. graminum Desm.

Spots slightly elongate, pale, fuscous-margined, limited by the

leaf veins; pycnidia seriate or scattered, brownish; conidia very slender, straight or curved, non-septate, multiguttulate, $55-75 \times 1-1.3 \mu$.

This is a frequent saprophyte or weak parasite on wheat, oats and numerous wild grasses. Under some conditions it becomes an injurious parasite, especially upon winter wheat.

***S. betæ* West.**

Spots pale brown, white in the center, brownish-margined; pycnidia epiphyllous, minute, black, prominent; conidia cylindric, straight or curved, white in mass.

It was noted causing a beet leaf spot.

***S. citrulli* E. & E.**

Spots small, round, white, scattered; pycnidia mostly solitary, one in the center of each spot, but slightly prominent; conidia cylindric or clavate-cylindric, $10-25 \times 1.5-2 \mu$.

On watermelon leaves.

***S. cucurbitacearum* Sacc.** is also on cucurbits.

***S. petroselini* Desm.**

Spots brown, in age white, amphigenous; pycnidia epiphyllous, minute, olivaceous, prominent; conidia filiform, straight or curved, $35-40 \times 1-2 \mu$. On parsley.

***S. apii* Chester** is very destructive on celery. The pycnidia are abundant in the leaf spots and in the case of stored celery they are found scattered over the blanched petioles.

***S. lycopersici* Speg.**

Spots large, often confluent and covering the entire leaf, sordid cinereous, subindeterminate; pycnidia scattered, hypophyllous, lenticular-hemispheric, prominent, membranous; conidia elongate, cylindric, $70-110 \times 3.3 \mu$, pluriseptate.

The cause of leaf spots of tomato.

***S. lactuæ* Pass.**

Spots irregular, brownish, angulate, sometimes destroying the



FIG. 330.—*S. apii*, pycnidium showing spores oozing through the ostiole. After Jensen.

entire leaf; pycnidia minute, punctiform, scattered, $90\ \mu$ in diameter; conidia filiform, straight or curved, $25\text{--}30 \times 1.7\text{--}2\ \mu$.

On lettuce.

S. consimilis E. & M.

Distinguishable from the preceding by the more indefinite spots, slightly larger pycnidia, $90\text{--}100\ \mu$, and longer conidia, $30\text{--}45 \times 2\text{--}2.5\ \mu$. It causes brown spots on lettuce leaves.

S. spadicea P. & C. causes a common twig blight of pine.

Pycnidia not spot-forming, becoming slightly erumpent on inner surface of browning needles, scattered, membranous, fuscous-olivaceous, subimmersed, $190\text{--}225\ \mu$ in diameter. Spores hyaline, cylindrical, slightly curved or flexuous, apex acute, 1-septate, rarely constricted at septum, $3\text{--}4 \times 30\text{--}45\ \mu$. Conidiophores short.

S. secalis P. & D.¹ is on rye. Pycnidia subepidermal, black, globose to subglobose, smooth, $85\text{--}130\ \mu$ in diameter; spores hyaline, 3-septate, usually curved and rounded at the ends, $2\text{--}3.5 \times 25\text{--}49\ \mu$.

S. passerinii Sacc. is on barley. Spores $1.7\text{--}3 \times 23\text{--}46\ \mu$, averaging $2.3 \times 34\ \mu$; pycnidia subepidermal, black, smooth, globose to subglobose, $80\text{--}150\ \mu$ in diameter; ostiole oval to elliptical, smooth, substomatal.

S. agropyri E. & E. is on *Agropyron repens*; **S. bromi** Sacc. on *Bromus inermis*.

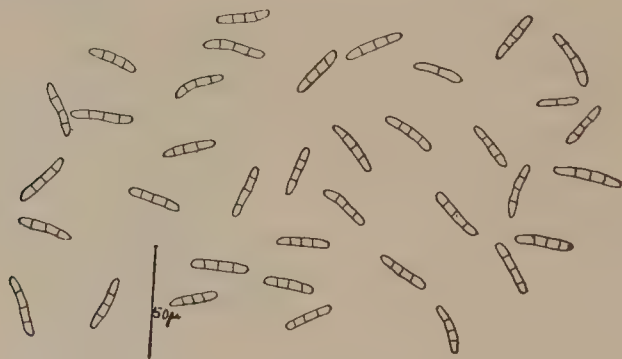


FIG. 331.—Spores of *S. nodorum*. After Weber.

S. nodorum Berk.^{2, 3} causes spotting of the glumes, glume blotch, and rachis of wheat.

¹ Weber, George F. Septoria disease of rye, barley, and certain grasses. *Phytop.* **13**: 1, 1923.

² Rosen, H. R. Septoria glume blotch of wheat. *Ark. Agr. Exp. Sta. Bul.* 175. 1921.

³ Weber, George F. Septoria diseases of wheat. *Phytop.* **12**: 537, 1922.

Pycnidia spherical, flattened or elongate, subepidermal, 160–210 μ in diameter; wall thin, soft, light brown, becoming dark brown or black; ostiole circular to oval, opening between the guard cells of the stomata; spores oblong, cylindrical, straight, curved or angularly bent, obtuse and rounded at the ends, hyaline, 3-septate, guttulate, 2–4 x 18–32 μ .

S. tritici Desm.¹

Pycnidia subepidermal, in substomatal chambers, globose to subglobose, in rows parallel to the vascular strands, brown to black, wall smooth, pseudo-parenchymatous, 1–3 cells thick, 80–150 μ in diameter; ostiole circular to oval, slightly raised, 12–20 μ in diameter; spores slender, cylindrical, hyaline, 3 to 7-septate, ends rounded, contents homogeneous or slightly guttulate, 1.75–2.7 x 39–70 μ .

On wheat causing speckled leaf blotch and killing many seedlings and tillers.

S. gladioli Pass.

Pycnidia 100–160 μ in diameter; conidia 3-septate, 20–55 x 2–4 μ , cylindrical, straight, hyaline.

On gladiolus causing disease on leaves and corms.

Other species are on cherry, plum, Citrus, grape, cranberry, rice, hemp, tobacco, cowpea, alfalfa, sweet potato, horse-radish, snapdragon, rose, hydrangea, iris, cyclamen, Sedum, Hedera, carnation, chrysanthemum, Kalmia, Azalea, phlox, narcissus, veronicas, hollyhock, sunflower, lily-of the-valley, oleander, chestnut, walnut, horse chestnut, sycamore, maple, ash, redbud, linden, Robinia, Spirea, dogwood, poplar, pecan.

Rhabdospora Montaigne (p. 355)

Pycnidia innate, erumpent, globose or depressed, brown or black; conidia as in Septoria.

Similar to Septoria, but on stems.

R. rubi Ellis. Pycnidia black, subglobose, innate, erumpent, scattered, 100–195 μ ; conidia linear, curved, 3 to 4-septate, 40–45 x 3 μ . On Rubus.

R. oxycocci Sh. is on cranberry.

Phleospora Wallroth (p. 355)

Pycnidia innate, imperfectly developed and chiefly formed of modified host tissue; conidia elongate-fusoid, thick, 2 to many-septate.

¹ Weber, George F. Septoria diseases of wheat. *Phytop.* **12**: 537, 1922.

This genus closely approaches the Melanconiales in structure. Several forms have been shown to be allied to *Mycosphærella*.

P. mori (Lév.) Sacc. on *Morus*=*Cylindrosporium mori*=*Mycosphærella*.

Several species occur as parasites on elm, mulberry, maple, sycamore, hawthorn.

Leptostromataceæ¹ (p. 335)

Pycnidia membranous or carbonous, black, more or less distinctly dimidiate, scutiform, astomous, ostiolate or cleft, erumpent or superficial. Over two hundred species.

Leptostromataceæ-Hyalosporæ

Conidia hyaline, 1-celled, globose to ovoid.

KEY TO GENERA OF **Leptostromataceæ-Hyalosporæ**

Pycnidia separate

Pycnidia not cleft

Conidiophores short or lacking, pycnidia without subicle; conidia muticate

Pycnidia gelatinous within..... 1. **Glœodes**, p. 360.

Pycnidia not gelatinous within, not stellate..... 2. **Leptothyrium**, p. 361.

Pycnidia more or less clearly cleft length-

wise, elongate or lanceolate..... 3. **Leptostroma**, p. 362.

Pycnidia in a stroma, phyllogenous..... 4. **Melasmia**, p. 362.

Glœodes Colby

Mycelium strictly superficial, dark colored, septate, profusely branched, often anastomosing, constituting a thallus, often fern-like in appearance but occasionally of other types; pycnidia dimidiate, membrano-carbonous, interior gelatinous; paraphyses present; conidia oblong, one-celled, hyaline.

G. pomigena (Schw.) Colby²

Pycnidia dark brown, dimidiate, scattered or aggregated, superficial, rupturing irregularly; conidia oblong, sometimes slightly curved, one-celled, hyaline, 10-20 x 4-7 μ ; conidiophores short or lacking; paraphyses septate, gelatinous, slender, blunt, longer than the conidia.

¹ Diedicke, H. Die Leptostromaceen. Ann. Myc. 11: 172, 1913.

² Stevens. F. L. Bul. 10, Bishop Museum. 1925.

On fruits and stems of certain species of *Pyrus* causing sooty blotch. The conidial stage is rare.



FIG. 332.—Sooty blotch thalli of fern-like type. After Colby.

***Leptothyrium* Kunze & Schweinitz (p. 360)**

Pycnidia superficial or erumpent, dimidiate, scutiform, membrano-carbonous, black, coalescing or scattered, ostiole variable, structure cellular; conidia ovoid-oblong to fusoid.

Some one hundred species.

In part = *Gnomonia* and *Gnomoniella*.

L. alneum (Lév.) Sacc. on alder = *Gnomoniella tubiformis*.

L. pomi (M. & F.) Sacc.

The fungus usually reported under this name forms minute, sterile, superficial, black spots, the so-called fly-specks, on apple.

This fungus probably is an imperfect stage of one of the Hemisphaeriales. See p. 145.

L. oxycocci Sh.

Pycnidia black, dimidiate, amphigenous, scattered, subcoriaceous to coriaceous, irregularly subglobose, subepidermal, erumpent, rupturing irregularly;



FIG. 333. — *Leptothyrium oxycocci*. Four spores. After Shear.



FIG. 334. — *Leptothyrium oxycocci*. Section of a pycnidium, showing its dimidiate character. After Shear.

conidia subfusoid, sometimes slightly curved, pseudoseptate, 10–15 x 2.5–3 μ ; conidiophores simple, straight, tapering, slightly longer than the conidia.

On cranberry.

Others are on honeysuckle, maple, box, strawberry, pears, *Cereus*.

Leptostroma Fries (p. 360)

Pycnidia dimidiate, subsuperficial, applanate, elongate, black, more or less hysterioid; conidia ovate, elongate or allantoid.

In part = *Hysteriaceæ*. There are some sixty species.

L. larcinum Fcl. on larch = *Mycosphærella larcina*.

L. piricola B. & S. occurs on the pear.

L. punctiforme Wallr. is on willow.

Melasmia Léviellé (p. 360)

Pycnidia dimidiate, carbonous, black, often on an effused, black stroma; conidia allantoid.

In part = *Rhytisma*. Over twenty species.

M. acerina Lév. is the conidial form of *Rhytisma acerinum*. See p. 120; **M. punctata** S. & R. and **M. salicina** Lév. of the two corresponding *Rhytismas*. See p. 120.

Leptostromataceæ-Hyalophragmiæ

Conidia oblong to fusoid, hyaline, 2 to several-septate.

Entomosporium Léviellé

Pycnidia depressed, subglobose, not ostiolate, black; conidia 4-celled, cruciate, each arm 1-ciliate.

A genus of three species of parasites. In part = *Fabræa*.

E. mespili (DC.) Sacc. = *F. mespili*.

E. maculatum Lév. on pear and quince = *F. maculata*. See p. 112.

E. thumenii (Cke.) Sacc. occurs on hawthorn.

Excipulaceæ (p. 335)

Pycnidia membranous to carbonous, black, cup-shaped, patellate or hysterioid, at first more or less spherical but at length widely open, erumpent or superficial, glabrous or hairy.

Excipulaceæ-Hyalosporæ

Conidia hyaline, continuous, globose to oblong.

KEY TO GENERA OF Excipulaceæ-Hyalosporæ

- Pycnidia pilose or setose, cupulate; conidia
muticate..... 1. **Amerosporium**, p. 363.
- Pycnidia smooth or nearly so
- Pycnidia more or less cup-shaped or disciform, black, of cellular context; subglobose, irregularly dehiscent and collabent..... 2. **Dothichiza**, p. 364.
- Pycnidia valvately gaping; conidiophores typically branched..... 3. **Sporonema**, p. 364.

Amerosporium Spegazzini

Pycnidia subcupulate, setulose, conidia cylindric to ellipsoid. Some twenty-five species, chiefly saprophytes.

A. œconomicum E. & T.

Spots orbicular, 2-6 mm., white above with a reddish border, mostly entirely reddish below; pycnidia epiphyllous, erumpent, conic-hemispheric, broadly perforate above, beset with straight, spreading, grayish-black, septate bristles, 100-150 x 4 μ ; conidia oblong-fusoid, 18-27 x 4 μ .

Very common on cowpea leaves in circular spots, with dark pycnidia in concentric circles on white background.

Dothichiza Libert (p. 363)

Pycnidia erumpent, roundish, somewhat disculate, irregularly dehiscent; conidia elongate or cylindric. In part=Cenangium.

D. populea S. & B. parasitizes poplar.

Sporonema Desmazieres (p. 363)

Pycnidia subepidermal, erumpent, at first closed, then opening radiately; conidia ovate or cylindric.

S. platani Bäuml. on *Platanus*=*Gnomonia veneta*. See p. 196.

S. phacidioides Desm.=*Pseudopeziza trifolii*. See p. 111.

S. oxycocci Sh.



FIG. 335.—*Sporonema oxycocci* on cranberry leaf. After Shear.

Pycnidia amphigenous, excipuliform, thickened at the base, gradually disappearing above, immersed, erumpent, depressed-globose, gregarious or scattered, 50–100 μ , sometimes collapsing, rupturing irregularly by a slit or triangular split; conidia cylindric, straight, 17–19 x 3–4 μ ; conidiophores simple, oblong to subglobose, about one fourth the

length of the spore or less. On cranberry.

S. pulvinatum Sh. is also on cranberry.

Melanconiales¹ (p. 334)

Mycelium internal; true pycnidia never developed, the conidiophores form a stratum; strata typically bearing conidia in acervuli which are immersed or erumpent, black or light colored, waxy, corneous or even submembranous, accompanied by setæ or not; conidia variable.

The common name “anthracnose” is applied to any disease caused by a member of this order.

A single family **Melanconiaceæ**, which contains about forty-five genera and over twelve hundred species.

Melanconiaceæ-Hyalosporæ

Conidia hyaline, 1-celled, globose to oblong, rarely dilute colored.

¹ Edgerton, C. W. The Melanconiales. Trans. Amer. Mi. Soc. **31**: 243, 1912.

KEY TO GENERA OF *Melanconiaceæ-Hyalosporæ*

Conidia muticate

Acervuli not setose

Conidia not catenulate; masses gray
to black, rarely bright colored,
waxy or horny

Growing, for the most part, on
leaves or fruits.....

1. *Glœosporium*, p. 365.

Growing usually on twigs of trees
or shrubs.....

2. *Myxosporium*, p. 368.

Acervuli setose at margin; conidiophores
short, fasciculate.....

3. *Colletotrichum*, p. 369.

Glœosporium and *Colletotrichum* are prominent in pathology as the "anthracnose fungi" and cause many important diseases. The two genera, distinguished only by the occurrence or non-occurrence of setæ, contain many species which have been transferred from one of these genera to the other on this character, which is to some extent a variable one depending upon the supporting medium, conditions of growth and the particular strain of the fungus under observation.

Many form-species have been described solely on a basis of the hosts affected. Subsequent culture study, and cross inoculation has often failed to sustain these species so that many forms that were formerly considered as distinct are now grouped under one name. No satisfactory disposition of these forms can be made until their ascigerous stages are known and compared and their biologic relations investigated.

Such work as has been done (see page 190) leads rather to consolidation than to segregation of species.

For sake of clearness and convenience, mention is made below of many form species of these two genera under their old names, though the evidence now is that in many instances they should be consolidated with other species.

Glœosporium Desmazieres & Montaigne

Conidial layer subepidermal, disciform or pulvinate, usually erumpent, pale or fuscous; conidia ovate, rarely oblong; conidiophores needle-shaped.

In part=*Glomerella*, *Pseudopeziza*, *Gnomoniella*, *Gnomonia*, *Trochila*, *Physalospora*, *Calospora*.

There are several hundred species, many of them very important pathogens. The spores in germination commonly form dark colored, thick-walled chlamydospores and usually become 1-septate.

G. rufomaculans (Berk.) Thüm. on a large variety of hosts, *G. fructigenum* Berk. on many fruits, *G. ribicolum* E. & E. on Ribis, *G. rubi* E. & E. on Rubus, *G. psidii* on guava, *G. læticolor* Berk. on peaches and apples and *G. versicolor* B. & C. on peaches, *G. cingulatum* Atk. on privet, are probably identical with *Glomerella cingulata*. See p. 190.

G. salicis West. on Salix = *Pseudopeziza salicis*.

G. piperatum E. & E. on pepper = *Glomerella piperata*. See p. 194.

G. cylindrospermum (Bon.) Sacc. on Alnus = *Gnomoniella tubiformis*.

G. vanillæ Cke. on orchids = *Calospora vanillæ*.

G. macropus Sacc. on Cattleya = *Physalospora cattelyæ*.

G. cinctum B. & C. on orchids = *Glomerella cineta*.

G. paradoxum (de Not.) Fcl. on Hedera = *Trochila craterium*.

G. atrocarpi Del. on Atrocarpus = *Glomerella atrocarpi*.

G. nervisequum (Fcl.) Sacc. on sycamore = *Gnomonia veneta*. See p. 196.

G. ribis (Lib) M. & D. on Ribes = *Pseudopeziza ribis*. See p. 111.

G. caryæ E. & D. = *Gnomonia caryæ*.

G. ampelophagum (Pass.) Sacc. = *Sphaceloma ampelinum*.

Spots subcircular often confluent, from cortex of the berry, centers gray; margin dark or red. Acervuli subepidermal, minute, collected; conidia oblong, ellipsoid or ovoid, 5–6 x 2–3 μ , hyaline.

Small dark spots are produced on fruit, leaf or cane of grape. These later enlarge and show white centers with dark or even red borders. The mycelium lies just below the epidermis. On shoots the cambium is killed and cankers develop.

An ascigerous stage had been reported in Europe as *Manginia*.

G. musarum Cke. & Mass. is a common wound parasite on bananas.

Acervuli innate, erumpent, gregarious, rose-tinged; conidia elongate-ellipsoid, ends rounded, 10–12 x 4–5 μ , granular.

G. trifolii Pk.

Spots subcuticular, brown, suborbicular, concentrically zonate; conidia oblong to cylindric, obtuse, 15–23 x 4–6.3 μ .

The cause of dying of stems and leaves of clover.

G. caulivorum Kirch.

Caulicolous, spots forming long dark streaks, more or less sunken, blackish-bordered; acervuli minute; conidia curved, more or less pointed, $12-22 \times 3-5 \mu$.

The cause of serious anthracnose affecting stem, fruit and leaf of clover.

G. medicaginis E. & K.

Acervuli scattered, innate, blackish, rather large, visible on both sides of the leaf, opening below; conidia oblong, cylindric, granular, subhyaline, more or less narrowed at the middle, $15-30 \times 3-4 \mu$.

On withered leaves and stems of alfalfa, defoliating the lower part of the stem.

G. juglandis (Lib.) Mont. causes a common and serious leaf blight of the butternut.

G. fagi (D. & R.) West. is on beech.

Spots subcircular, fuscous above, olivaceous, vitreous beneath; acervuli small, prominent, honey-colored; conidia oblong ovate, $15-20 \times 7-8 \mu$, minutely 1 to 3-guttulate; conidiophores fasciculate, cylindric, fuscous.

G. apocryptum E. & E. causes a nursery disease of maples and of box elder.

Acervuli numerous, minute, mostly hypophyllous, on dead areas of the leaf; conidia very variable in size, $5-12 \times 2.5-5 \mu$, oblong to narrowly elliptic.

G. betularum E. & M.

Spots rounded, 2-3 mm., blackish margined; acervuli amphigenous, brownish, $120-140 \mu$, becoming cupulate; conidia hyaline, obovate, $9-10 \times 5-6 \mu$.

It is common on leaves of American birches.

G. ulmicolum Miles. Spots epiphyllous, raised, gray, elongated, following the leaf veins, often extending the entire length of the secondary veins which have become browned far beyond the limits of the spot; acervuli epiphyllous, gregarious, subcutaneous, covered by the persistent, darkened cuticle which finally ruptures irregularly to allow the dispersal of the spores, averaging 800μ in diameter, irregular in outline but usually elongated suborbicular; conidiophores in a closely packed layer, dilute-brown, cylindrical, on a pseudo-parenchymatous, colorless hymenial base, $10-15 \times 2-3 \mu$, terminating in a sterigma-like projection on which the spores are borne; conidia hyaline, one-celled, straight, rounded at both

ends, oblong-cylindrical, ovate, elliptical or pyriform, 8–10 x 3–5.5 μ .

Parasitic on leaves of elm.

Other species have been reported on persimmon, strawberry, almond, cranberry, egg-plant, cucurbits, alfalfa, cabbage, carnation, clematis, rose, orchids, Ficus, violet, Pelargonium, Anthurium, begonia, oak, elm, palm, linden, beech, ash, birch, butternut, hazel, hickory, horse chestnut, maple, pecan, sycamore, willow, poplar, alder, Carpinus, Corylus, Paulownia, barberry.

Myxosporium Link (p. 365)

Acervuli immersed or superficial, indefinite, pallid or reddish; conidia ovate, hyaline or pale, conidiophores slender-cylindric.

About seventy species, some of which are important pathogens.

In part = *Gnomonia*. See p. 196.

M. valsoideum (Sacc.) All. on sycamore = *Gnomonia veneta*. See p. 196.

M. corticolum Edg.

Acervuli erumpent, originating under several layers of cortex, 1–2 mm. in diameter, scattered over the diseased area; conidia



FIG. 336.—*M. corticolum*, on apple twig.
After Edgerton.

straight or curved, cylindric, very densely granular, 18–36 x 6–9 μ , oozing out of the pores in white cirri; conidiophores very short.

It forms bark cankers in pear and apple in America.

M. acerinum Pk. is often fatal to maple trees.

Other parasitic species are on Liriodendron, pear, sycamore, apple, conifers, beech, oak, maple.

Colletotrichum Corda (p. 365)

Acervuli innate, erumpent, discoid or elongate, dark, bearing long black setæ; conidia terete to fusoid; conidiophores short.

The genus is distinguished from *Glœosporium* by the presence of setæ, a somewhat unreliable character. See p. 365.

In part=*Glomerella* and *Pseudopeziza*. See pp. 110, 190.

Some eighty species, several of them very important plant pathogens.

C. gossypii South. on cotton=*Glomerella gossypii*. See p. 194.

C. lindemuthianum on beans=*Glomerella lindemuthianum*. See p. 193.

C. falcatum Went.

Acervuli poorly defined, setæ irregularly arranged, cuspidate, $100-200 \times 4 \mu$, brownish; conidia falcate, $25 \times 4 \mu$; conidiophores ovoid, $20 \times 8 \mu$, hyaline to fuscous.

This is believed to be the chief cause of the red rot of sugar-cane.

C. cereale Manns

Spots circular to ovoid, 30 mm.; acervuli dark brown or black; setæ few or many, dark brown to black, at base $6-8 \mu$ thick,

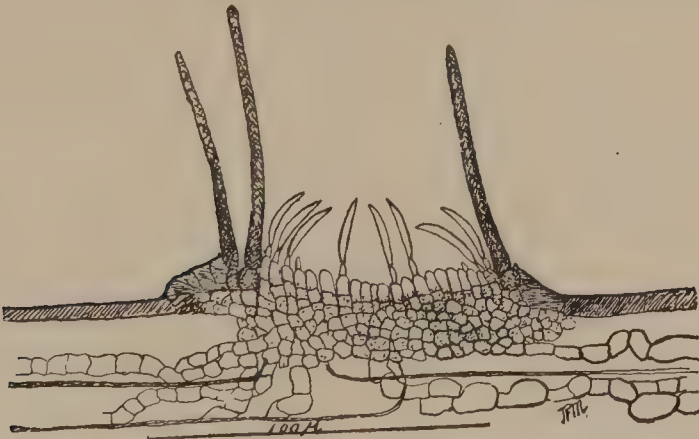


FIG. 337.—*C. cereale*, acervulus showing mycelium, setæ, conidiophores and spores. After Manns.

tapering to a length of $60-120 \mu$, continuous or 1 to 2-septate; conidia $18-26 \times 3-4 \mu$, spindle to boat-shaped, 2 to several-guttulate; conidiophores very short, $12-6 \times 1-2 \mu$.

This fungus is parasitic on the roots, stems, blades and spikes of rye, wheat, oats, barley, emmer, orchard grass, timothy, blue grass and chess. The disease causes a premature ripening and

shrivelling of the grain. Superficially the diseased heads present the same appearance as those attacked by scab but no pink overgrowth is present, nor is the presence of the disease always apparent, as it was found on numerous heads of grain which appeared to be healthy. Morphological studies indicate that all the hosts mentioned above are affected by the same fungus.

C. glæosporioides Penz. (= *Glomerella cingulata*) is found on Citrus, causing wither-tip.

C. lagenarium (Pers.) E. & H. see p. 194.

C. trifolii Bain

Spots dark, depressed; acervuli erumpent, scattered or gregarious; conidia straight, ends rounded, $3-4 \times 11-13 \mu$; conidiophores cylindric or fusoid, hyaline; setæ few or many, continuous or uniseptate, dark, paler apically, $4-7 \times 39-62 \mu$, sinuous, or nodose.

It occurs as an anthracnose producer on stems, rarely on leaves, of clover and alfalfa.

C. spinaciæ E. & H.

Spots roundish, dirty-white or greenish, 2-4 mm., with a slightly raised border; acervuli amphigenous, punctiform, $40-75 \mu$, with 3-12 erect or spreading, bristle-like setæ, $60-75 \times 4-4.5 \mu$, subbulbous at base, subhyaline, subacute above, dark brown below; conidia subfalcate, fusoid, 2 to 4-guttulate, $14-20 \times 2.5-3 \mu$, ends subacute; conidiophores short.

It produces blotches on spinach leaves.

C. phomoides (Sacc.) Ches.

Spots depressed, circular, slightly discolored, center black, 5-10 mm., later irregular and confluent; acervuli abundant, densely gregarious, rusty brown to black, applanate, $95-150 \mu$; setæ abundant, fuliginous, generally curved, septate, $65-112 \mu$; conidia oblong, $16-24 \times 4 \mu$, ends subacute; conidiophores short, slender, $30-40 \mu$ high, arising from a well developed stroma. On tomato.

This is a common cause of ripe rot of tomatoes.

C. nigrum, E. & H.

Spots blackish, depressed, decayed; acervuli numerous, superficial; setæ numerous, slender, pointed; conidia oblong. On peppers.

C. erumpens (Sacc.) does damage on rhubarb.

C. malvarum Br. & Casp. (= *C. althæa*.)

Epiphyllous and cauliculous; spots brown, sunken; acervuli

erumpent; setæ dark brown, abundant, 1 or 2-septate, usually colorless below, $60-109 \times 3-5 \mu$, appearing after the conidiophores which are colorless, cylindric, tapering slightly and apically rounded, slightly longer than the conidia; conidia irregular, oblong, granular, flesh-colored in mass, $11-28 \times 5 \mu$.

The cause of anthracnose of the hollyhock.

C. violæ-tricoloris R. G. Sm.

Spots pale-yellow on leaves. Dead areas on petals occur with more or less deformity of blossom. Spots at first orbicular and definite, later confluent and irregular, acervuli numerous, $50-150 \mu$, often confluent; stroma usually poorly developed; setæ mostly single or in pairs, $20-70 \mu$, deep brown, 1 to 2-septate, tapering gradually to a point; conidia oblong or slightly curved, ends blunt, $20 \times 5 \mu$; conidiophores short, hyaline.

It causes spotting of pansy leaves and consequent failure to bloom.

Other species are on grape, turnip, pea, agave, orchids, Anthurium, cacao, Ficus, primrose, palms, Aspidistra, snapdragon, Cyclamen, Dracæna, coffee.

Melanconiaceæ-Phæosporæ

Conidia dark, continuous, globose to oblong or fusoid.

Melanconium Link

Acervuli subcutaneous, conic or discoid, black; conidia not catenulate, elongate to globose-oblong, erumpent in black masses; conidiophore simple. In part=Trichosphaeria. See p. 160.

More than one hundred fifty species.

M. fuligineum (Scrib. & Viala) Cav.

Acervuli scattered or gregarious, at first gray-cinereous, then brownish, subepidermal, erumpent; conidia ovoid to ellipsoid, inequilateral, acute $9-12 \times 4-6 \mu$, olive, guttulate; conidiophores filiform, from a well developed stroma.

It causes the important bitter rot of ripening grapes, especially the white varieties, occurring also on shoots and peduncles. Acervuli appear on the surface of the rotted berries. The mycelium penetrates even to the seeds.

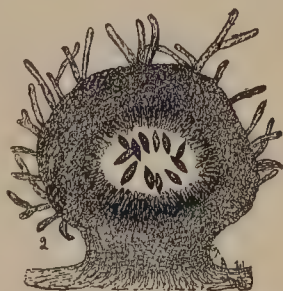


FIG. 338.—*M. fuligineum*.
After Atkinson.

M. pandani Lév. is common on *Pandanus* in greenhouses, killing the branches.

M. sacchari Mass.

Acervuli numerous, collected in indeterminate, pallid, orbicular spots; conidia cylindric, $10-15 \times 3-4 \mu$, straight or slightly curved, olivaceous, smooth.

In leaves, sheaths and culms of sugar cane.

Melanconiaceæ-Hyalodidymæ

Conidia hyaline, 1-septate, ovoid to fusoid.

Marssonina Fisch.

Acervuli globose-discoid, pale, conidia ovate to elongate, muciculate. In part=*Gnomonia*, *Trochila*, *Pseudopeziza*.

Some seventy-five species, all leaf parasites, several of economic importance.

M. castagnei (D. & M.) Sacc. on poplar = *Trochila popularum*.

M. juglandis (Lib.) Sacc. on walnut = *Gnomonia leptostyla*. See p. 198.

M. populi (Lib.) Sacc.

Spots suborbicular, epiphyllous, separate or confluent, brown,

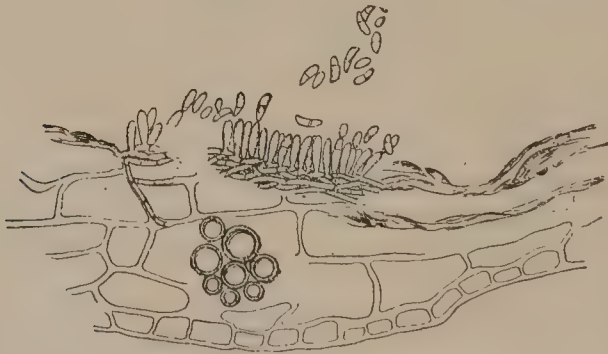


FIG. 339.—*M. panattoniana*, cross section of an acervulus. After Brandes.

darker margined, acervuli convex to applanate, fulvous; conidia obovate to subpyriform, $20 \times 12 \mu$, constricted at the septum, straight or curved.

On poplar, injurious in nurseries.

M. panattoniana (Berl.) Mag.¹ = *Marssonia perforans* E. & E. = *Didymaria perforans* (E. & E.) Dandeno.

Spots small, irregular, 1-2 mm., pale, soon deciduous; acervuli 100-120 μ , or by confluence larger; conidia abundant, clavate or wedge shaped, 11-15 x 2.5-3 μ .

The cause of leaf perforations of lettuce.

M. violæ (Pass.) Sacc.

Discoloration of the host slight, acervuli numerous, scattered, small; conidia curved or straight, 15-18 x 5-6 μ , septum usually excentric.

Small spots are produced on violet leaves.

Others are on strawberry, rye, rose, oak, ash, butternut, chestnut, hickory, poplar, walnut, willow.

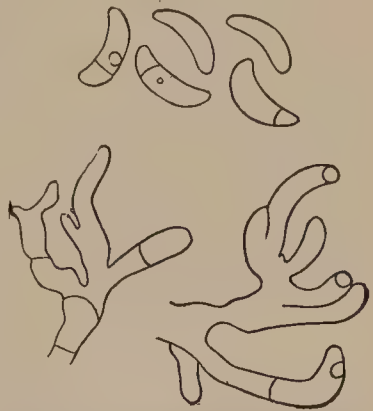


FIG. 340.—*Marssonina violæ*. Spores and conidiophores. After Jones and Giddings.

Melanconiaceæ-Hyalophragmiæ

Conidia hyaline, 2 to several-septate, oblong to fusoid or clavate.

Septoglœum Saccardo

Acervuli very small, subepidermal, erumpent, pallid; conidia oblong, separate, muciculate. Some twenty-five species of leaf parasites.

S. profusum (E. & E.) Sacc. Spots epiphyllous, flavous; acervuli scattered, hypophyllous, large; conidia issuing in white cirri, cylindrical, oblong, granular, 3-septate, 25-30 x 6-7 μ . On living leaves of elm and on *Corylus americana*.

S. hartigianum Sacc. attacks maple, killing very young twigs.

S. cydoniæ (Mont.) Pegl. is on the quince; **S. fraxini** Hark. on ash.

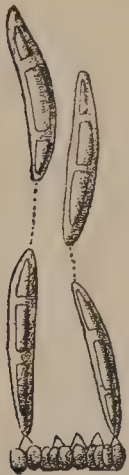


FIG. 341. — *Septoglœum acerinum*, conidiophores and conidia. After Saccardo.

¹ Brandes, E. W. Anthracnose of lettuce caused by *Marssonina panattoniana*. Jour. Agr. Res. 13: 271, 1918.

Melanconiaceæ-Phæophragmiæ

Conidia dark, 2 to several-septate, oblong to cylindric.

KEY TO GENERA OF Melanconiaceæ-Phæophragmiæ.

Conidia muticate

Conidia not in chains, oblong, not stellate,
not rostrate, not protruded in cirri. 1. *Coryneum*, p. 375.

Conidia ciliate at apex

Conidia 1-ciliate. 2. *Hyaloceras*, p. 374.

Conidia several-ciliate. 3. *Pestalozzia*, p. 374.

Hyaloceras Dur. & Mont.

Monochaetia Sacc.

As in *Pestalozzia* except that the conidia bear only a single seta. About sixty species.

H. pachysporum (Bub.) Bub. is common on chestnut causing large, circular, dead leaf spots with the acervuli showing in somewhat concentric circles.

Pestalozzia de Notaris¹

Acervuli subcutaneous, erumpent, discoid or pulvinate, black; conidia elongate, colored or the endcells hyaline, with several hyaline setæ on each end.



FIG. 342.—*P. funerea*. A. Spores. B. A young mycelium. C. Hypha of an older mycelium. After Reed.

A genus of over two hundred species of various habit, some of considerable economic importance.

P. hartigii Tub. causes disease of tree and shrub seedlings in nurseries, constricting the stem just above the soil and resulting in death.

P. funerea Desm.

Acervuli scattered, punctiform, blackish, subepidermal, erumpent; stroma depressed, white; conidia oblong, fusoid, 5-celled, constricted at the septa, the three central cells fuscous, the others hyaline, $22-32 \times 6-8 \mu$, with 2-5 recurved, hyaline spines, $10-15 \times 0.7-1 \mu$; conidiophores short, $5-9 \times 1-1.5 \mu$.

¹ Klebahn, H. Zur Kritik einiger Pestalozzia-Arten. Myc. Cent. 4: 1, 1914.

It is found on various conifers causing disease; also a stem spot of ginseng, girdling the petioles.

***P. guepini* Desm. var. *vaccinii* Sh.**

Acervuli minute, punctiform, convex, black, subepidermal, erumpent; conidia elliptic and somewhat unequilateral, about $20\ \mu$ long; central cells dark, the two end cells hyaline, the apical cell with 3–4 filiform setæ $22\text{--}35\ \mu$ long, the basal with a short hyaline appendage $6\text{--}12\ \mu$ long.

Common on fallen leaves of cranberries, and associated with rot of the berries.

***P. uvicola* Speg.**

Acervuli globose, lenticular, black, subepidermal, erumpent, $300\text{--}400\ \mu$; conidia fusiform, 5-celled, the three median olivaceous-fusoid, the others hyaline, $35 \times 8\text{--}10\ \mu$, inferior appendage $25\text{--}30 \times 1\ \mu$, superior group $8\text{--}10 \times 1\ \mu$.

It is described as the cause of rot of grape berries and of a leaf spot on the vine.

It is described as the cause of rot of grape berries and of a leaf spot on the vine.

Others are on sugar cane, calla, rose, fir, palms, willow, *Lupinus*, eucalyptus, sycamore, linden.

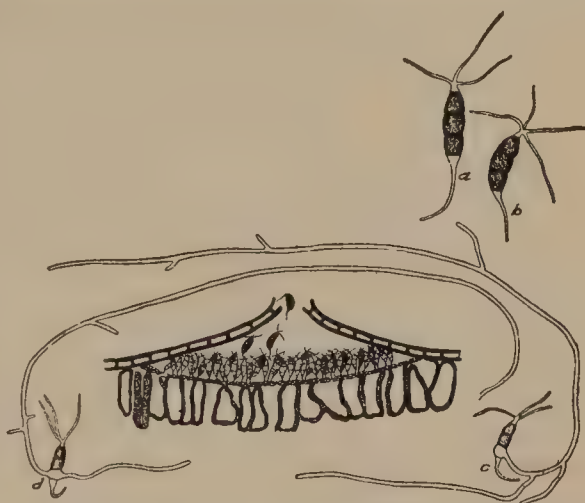


FIG. 343.—*Pestalozzia guepini vaccinii*; *a*, a conidium having an apical appendage with three branches; *b*, a conidium having an apical appendage with four branches; *c*, a germinating conidium; *d*, a germinating conidium sending out two germ tubes. After Shear.

***Coryneum* Nees (p. 374)**

Acervuli discoid or pulvinate, subcutaneous, erumpent, black, compact; conidia oblong to fusoid.

***C. beyerinckii* Oud. = *Ascospora beyerinckii*, see p. 165.**

***C. foliicolum* Fel.**

Spots epiphyllous, ochraceous, indefinite; acervuli punctiform, erumpent; conidia ellipsoid-oblong, $17 \times 6\text{--}7\ \mu$, 3-septate, constricted at the septa, olivaceous, lower cell subhyaline, stalk subhyaline, $15\text{--}20 \times 1.25\ \mu$.

It is present as a saprophyte on apple leaf spots.

C. tumoricolum Pk. Spots scattered, suborbicular, pale, bounded by a red-brown border. On living leaves of elm.

Melanconiaceæ-Scolecosporæ

Conidia cylindric, filiform or subballantoid, hyaline, mostly continuous.

Cylindrosporium Unger

Acervuli subepidermal, white or pallid, disciform or subeffuse; conidia solitary, in mass pale, filiform, continuous, hyaline, straight or curved.

About one hundred species of parasites, several of them of considerable economic importance.

C. mori Berl. on mulberry = *Mycosphærella morifolia*.

C. castanicolum (Desm.) Berl. on chestnut = *Mycosphærella maculiformis*.

C. padi Karst. on *Prunus* = *Coccomyces*. See p. 117.

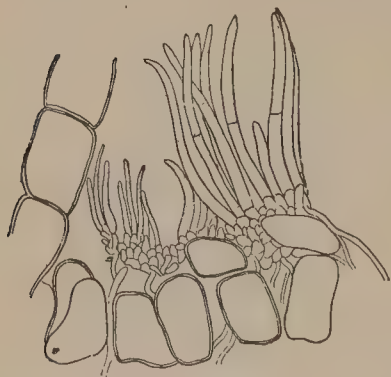


FIG. 344.—*C. padi*, section of acervulus. After Pammel.

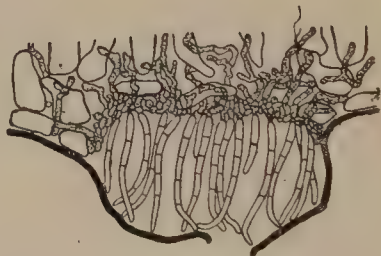


FIG. 345.—*C. juglandis*, acervulus with conidia. After Wolf.

C. chrysanthemi E. & D.

Spots subindefinite, 1 cm. or more broad, black; acervuli innate, amphigenous, 100–170 μ ; conidia fusoid-straight, 50–100 x 3–4.5 μ .

The fungus causes dark blotches on the leaves of chrysanthemum.

C. clematidis E. & E.

Spots amphigenous, reddish-brown, round or subangular, 1–3 μ ; acervuli comparatively few, epiphyllous, immersed, scattered; co-

nidia fusoid-linear, 75–80 x 2.5–3 μ , somewhat curved, exuding in a white mass. It causes leaf spot of Clematis.

C. juglandis Wolf causes leaf spot on walnut. Acervuli erumpent, conidia clavate, many-septate, 20–50 x 3–3.8 μ .

C. ulmicolum E. & E. Spots becoming flavous; acervuli minute, hypophyllous; conidia cylindrical, 45–65 x 4 μ , hyaline. On leaves of elm. In spite of the differences in spore measurements, the possibility has been suggested that this is not different from *Phleospora ulmi*.

Others are on hop, lily, maple, alder, birch, elm, hackberry, locust, walnut.

Moniliales (p. 334)

The Moniliales differ from the Sphærospidales in the absence of the pycnidium and from the Melanconiales in their somewhat loose, separate hyphæ, not innate and closely aggregated as in the Melanconiales. There are genera on the boundaries between these orders which are difficult to place, as for example *Coryneum*, some species of which are often put in *Helminthosporium*; *Vermicularia* which sometimes is confounded with *Volutella*, etc.

The order is one of very great diversity and contains a multitude of forms. Many are only saprophytes while some are aggressive parasites.

KEY TO FAMILIES OF Moniliales

Hyphæ in more or less loose cottony masses

Hyphæ and conidia clear or bright colored.....

I. **Moniliaceæ**, p. 378.

Hyphæ and conidia typically both dark; one or the other always dark.....

II. **Dematiaceæ**, p. 396.

Hyphæ compactly united or forming a globose to cylindric body which is often stalked

Hyphal body cylindric to capitate, stalked, i. e., a synnema or coremium.....

III. **Stilbaceæ**, p. 416.

Hyphal body more or less globose, sessile, i. e., a sporodochium.....

IV. **Tuberculariaceæ**, p. 418.

Moniliaceæ (p. 377)

Hyphæ hyaline or bright colored, more or less fragile, lax, not cohering in fascicles; conidia concolorous, hyaline or bright colored.

Moniliaceæ-Amerosporæ

Conidia continuous, globose or ovoid to short cylindric.

KEY TO GROUPS OF Moniliaceæ-Amerosporæ

- Hyphæ very short or obsolete, little different from the conidia
 Conidia in chains..... 1. **Oösporeæ**, p. 378.
- Hyphæ elongate and distinct from the conidia
 Conidiophores simple or little branched, apically swollen, conidia in heads
 Conidia not in chains..... 2. **Cephalosporiæ**, p. 379.
 Conidia in chains..... 3. **Aspergilleæ**, p. 380.
- Conidiophores much-branched, conidia not in heads
 Conidia borne irregularly on simple or branched but not inflated or verticillate conidiophores..... 4. **Botrytideæ**, p. 384.
 Conidia borne on verticillately branched conidiophores..... 5. **Verticillia**, p. 389.

Oösporeæ¹

Conidiophores short or obsolete, conidia in chains.

KEY TO GENERA OF Oösporeæ

- Conidial chains arising at the apex of the hyphæ
 Conidia globose, elliptic or ovate, all of equal size; sterile hyphæ evident; conidia not connected by an isthmus
 Growing within the substratum; haustoria none..... 1. **Monilia**, p. 379.
 Growing on the surface of living plants... 2. **Oidium**, p. 379.

¹Sumstine, R. Studies in North American Hyphomycetales. The tribe Oösporeæ. *Mycol.* 5: 45, 1913.

Monilia Persoon (p. 378)

Hyphæ erect, branched, forming a dense mycelial felt which produces numerous conidiophores; conidia catenulate, hyaline or light-colored, ovate or lemon shaped.

Various form species are known to belong to the genus *Sclerotinia*. See p. 101.

Oidium Link (p. 378)

On the surface of living leaves; hyphæ branched, white, bearing erect, simple conidiophores with catenulate, ovoid conidia.

These conidial fungi in the main belong to the *Erysiphaceæ*, (see p. 127) though some forms are placed in *Oidium* which clearly do not belong to that ascigerous family. Salmon states that there are some forty-four apparently *Erysiphaceous* *Oidiums* listed; but that twenty-five of these grow on plants known to be the hosts of ascus bearing *Erysiphaceæ*.

The following unconnected forms may be mentioned:

O. erysiphoides Fr. on hop, clover, cucumber, etc.;

O. chrysanthemi Rab. on chrysanthemums;

O. mespilinum Thüm on *Mespilus*;

O. tabaci Thüm on tobacco;

O. verbenæ T. & B. on *Verbenas*;

O. quercinum Thüm on oaks.

Cephalosporieæ (p. 378)

Hyphæ elongate; conidia in heads.

Trichoderma Persoon

Sterile hyphæ decumbent, cespitose; fertile branches ascending, not inflated at the apex, several times forked; conidia capitate, globose or oblong, sessile on the head.

T. koningi Oud.

Conidia elliptical, $3-4 \times 2.5-3 \mu$.

It causes storage rot of sweet potatoes and is also destructive on apple roots.

Cephalosporium Corda

Hyphæ creeping, conidiophores short, erect, not apically swollen. Conidia spherical or ovate, hyaline or slightly colored.

The small-spored conidial forms often associated with *Fusarium* (microconidia) belong to this form-genus.

Cephalosporium acremonium has been closely associated with a black bundle disease of corn.¹

Aspergilleæ (p. 378)

Hyphae well developed; conidia in heads, catenulate.

KEY TO GENERA OF **Aspergilleæ**

Fertile hyphae inflated at apex, simple or nearly so

Sterigmata of apical vesicle none or simple; conidia terminal on sterigmata

1. **Aspergillus**, p. 380.

Sterigmata verticillately branched.

2. **Sterigmatocystis**, p. 380.

Fertile hyphae little or not at all inflated, verticillately branched at tip; tips unequally verticillate; conidia globose, without mucus; conidiophores slender

3. **Penicillium**, p. 381.



FIG. 346.—*Aspergillus*.
From Strassburger et al., Text Book of Botany.

Aspergillus (Micheli) Link

Hyphae effused, creeping; conidiophores erect, simple, capitate; conidia catenulate; sterigmata none or indistinguishable from the conidia.

The conidia are often found, the asci but rarely.

A. ficuum (Hen.) Weh. and **A. phoenicis** (Cda.) Lind. occur on figs.

A. niger v Tieg.² occurs on onions.

Grove erects a new genus *Rhopalocystis*,³ for this species, based on the fact that its color should place it in the *Dematiaceæ*.

Sterigmatocystis Cramer

As in *Aspergillus* but with the sterigmata branched in whorls at the apex.

S. castanea Pott. causes an internal rot of pomegranates.

¹ Reedy, C. S. Holbert, J. R., The black-bundle disease of corn. Jour. Agr. Res. **27**: 177, 1924.

² Thom, Charles. *Aspergillus niger* group. Jour. Agr. Res. **7**: 1, 1916.

³ Grove, W. B. Four little-known British fungi. Jour. Econ. Biol., **6**: 38, 1911.

Penicillium Link ¹ (p. 380)

Hyphæ creeping; conidiophores erect, apically irregularly verticillate-penicillately branched; conidia catenulate, spherical, or elliptical, hyaline or variously colored. For the ascigerous stage see page 125.

The species within this form genus are generally difficult of description and recognition requiring their culture on media of definite composition under strictly controlled conditions, observation of the habit, structure, and appearance of the colony on two different, standard media and of the physiological effects of the colony upon these media, as well as full note of habit and morphology. Many of the forms are cosmopolitan and indiscriminate saprophytes. The two species given below as on oranges are, however, characteristic of this substratum. The following descriptions are taken from Thom.

P. expansum Link (in part), emend Thom, = *Coremium* glau-



FIG. 347.—*P. expansum* Link: a, b, f, branching and arrangement of branches of conidial fructification; c, d, e, conidiiferous cells and conidial chains; g, h, j, k, l, sketches of fructification; m, n, o, germination of conidia. After Thom.

cum Link. = *Penicillium* glaucum Link (in part), = *Coremium* vulgare Corda (in part).

Colonies upon gelatine and potato or bean agar, green becoming gray-green and slowly brown in several weeks, floccose, with concentric zones tufted with short, loose, coremium-like aggregations

¹ Thom, C. Cultural studies of species of *Penicillium*. U. S. Dept. of Agr. Bur. Animal Ind. Bul. 118, 1910.

of conidiophores, not over 1–2 mm. in height except in old cultures containing sugar, broadly spreading with broad white margin in growing colonies. Reverse somewhat brown. Conidiophores either very short lateral branches of ærial hyphæ or very long, 1 mm. or more, arising singly or grouped with others to form coremia. Conidial fructifications consist of 1 to 3 main branches bearing verticils of branchlets supporting crowded whorls of conidiiferous cells, 130–200 x 50–60 μ at base, in cultures without sugar; in sugar media continuing for some weeks to produce great number of conidia which come to form masses perhaps 1 mm. in thickness. Conidiiferous cells 8–10 x 2–3 μ . Conidia elliptical to globose, 2 x 3.3 or 3–3.4 μ , green, homogenous, persisting in chains when mounted. Colonies begin to liquefy gelatine slowly after about 10 days and continue until it is completely liquefied.

It occurs characteristically upon decaying apples and other pomaceous fruits, where old colonies often produce coremia 1 cm. or more in length and very large.

Thom further states:

“I find there is a group of strains giving the general morphology and general physiological reactions described by me under the name *expansum*. These organisms vary somewhat in their rate of activity, slightly in color of spore area and more considerably in the colors induced in the substratum, yet they have an essential homogeneity in the cultural picture. The difficulties of separating these organisms into identifiable species have led me thus far to hold the nomenclature last used, *P. expansum*, for the entire lot. It has been possible to produce some rot in apples by organisms outside this group but the amount of rot so induced and the observations that I have made in the rotten-apple barrel do not lead me to believe that under ordinary conditions in storage the *Penicillia* outside the *P. expansum* series are of great importance.”

Many citations in the literature to *P. glaucum* Link and *P. crustaceum* (L.) Fries refer to this species.

***P. italicum* Wehmer**

Colonies on plain gelatine and potato or bean agar bluish green, becoming gray-green when old, broadly spreading, ærial portion composed at the broad margin almost entirely of conidiophores, but becoming slightly floccose in the center. Reverse of colonies dark brownish, often almost black in media containing sugar. Conidiophores from short, 100 μ , to very long, 600 μ , averaging per-

haps $250\ \mu$, arising either directly from substratum or as branches of aërial hyphæ. Conidial fructifications up to $300\ \mu$ or more in length, consisting usually of a main branch and one lateral branch, each producing a whorl of branchlets bearing crowded verticils of conidiiferous cells, $12\text{--}14 \times 3\ \mu$. Conidia breaking off in masses in handling old cultures, which rise in clouds when shaken. Chains of conidia loosely divergent, long; conidia $2\text{--}3 \times 3\text{--}5\ \mu$, cylindrical to elliptical or slightly ovate, clear green by transmitted light. Masses of spores continue to increase from 2 to 3 weeks. Petri-dish colonies partially and slowly liquefy gelatine (12 to 20 days). Numerous white sclerotia are produced upon the surface of the medium after 2 to 3 weeks' growth, especially upon fruits and other acid media rich in sugar.

Cosmopolitan; characteristic of decaying oranges, which become bright blue-green with this mold as contrasted with the olive-green species which is often associated with it upon the same fruit.

***P. digitatum* Sacc.**

Colonies on sugar gelatine and potato or bean agar grayish olive, irregularly shaped from the unequal growth and branching of rather few hyphæ; aërial portion consisting only of very short conidiophores and conidia. Reverse of colony commonly brown to black. Conidiophores rising directly from the substratum, $30\text{--}100 \times 4\text{--}5\ \mu$, usually very short. Conidial fructification a few tangled conidial chains up to $160\ \mu$ in length, borne upon conidiiferous cells $13\text{--}16 \times 3\text{--}4\ \mu$. Conidia cylindrical to almost globose,

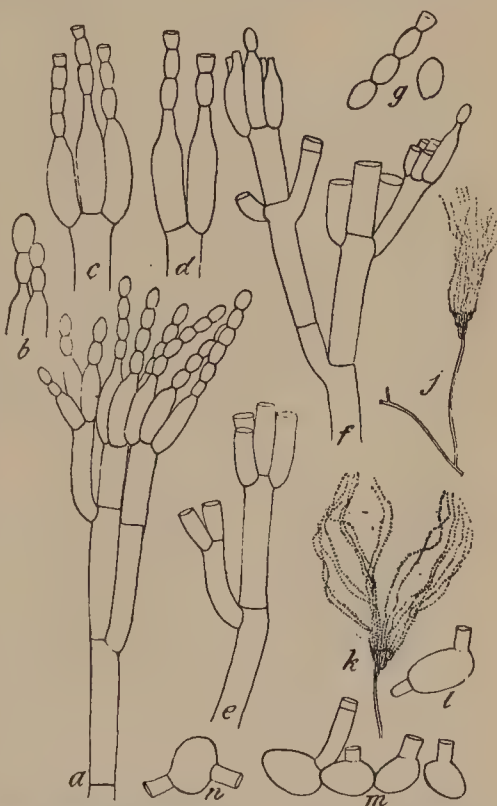


FIG. 348.—*P. italicum*; a, b, c, d, e, f, g, types of branching formation of verticils of conidiiferous cells and conidial chains, j, k, sketches of conidial fructifications; l, m, n, swelling and germination of conidia. After Thom.

4-7 x 6-8 μ , often uneven in size and shape in the same chain. Colonies do not liquefy sugar gelatine except occasionally in old cultures; litmus reaction acid; grows readily on organic media,

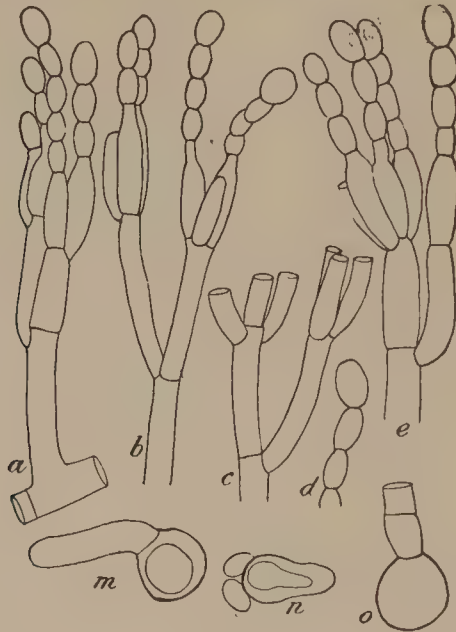


FIG. 349.—*P. digitatum*: a whole conidiophore and fructification; b, c, d, e, types of branching and formation of conidia; m, n, o, germination of conidia. After Thom.

but shows a very pronounced affinity for such media with high percentages of sugar, in which it produces a strong odor. Refused to grow in synthetic media containing nitrogen as sodium nitrate.

Cosmopolitan upon citrus fruits, distinguished from *P. italicum* by the sharp contrast of its olive color with the blue of the other.

Botrytideæ (p. 378)

Conidiophores elongate, simple or branched but not inflated, and the branches not verticillate; conidia borne variously, globose or ovate to elliptic.

KEY TO GENERA OF Botrytideæ

Conidia smooth or scarcely roughened,
acrogenous or pleurogynous, intermediate
joints of the conidiophores equal, conidia-
bearing hyphæ of one sort only

- Fertile hyphæ simple or nearly so, hyphæ not denticulate; conidia solitary, sterile hyphæ within the host. 1. *Ovularia*, p. 389.
- Fertile hyphæ branched; conidia globose to ovoid
- Both sterile and fertile hyphæ procumbent; sterile hyphæ superficial, fertile hyphæ vaguely branched; conidia acro-pleurogynous. 2. *Sporotrichum*, p. 385.
- Fertile hyphæ erect or ascending; conidia loosely grouped about the apex, not involved in mucus; apices not muriculate or inflated. 3. *Botrytis*, p. 385.

Sporotrichum Link

Hyphæ widely spreading, much branched; conidiophores simple, short; conidia solitary or in groups on separate sterigmata, ovoid or subglobose.

Over one hundred twenty-five species are described, most of which are saprophytes.

S. poæ Pk.

Hyphæ creeping, interwoven, branched, continuous or sparingly septate, variable in thickness, 2.5–6 μ , hyaline, forming a loose cottony stratum; conidia of two kinds; microconidia, globose or broadly ovate, 4–12 μ ; macroconidia abundant, elongate elliptic to ovate elliptic, 1, rarely 2-septate, about three or four times as large as the microconidia.

The form is an atypical one in that it produces two kinds of spores; one kind which is usually septate.

It is the cause of bud rot of carnations; also found in connection with a disease known as "silver top" of June grass in which the panicles wither as they expand.

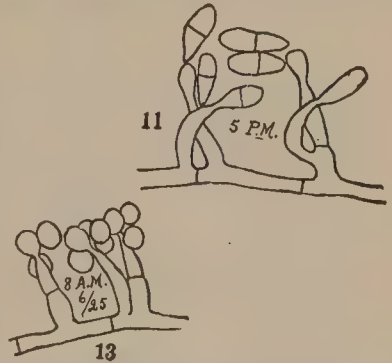


FIG. 350.—*S. poæ*. 11, Hypha bearing conidiophores and macroconidia. 13, Hypha bearing conidiophores and microconidia. After Heald.

Botrytis (Micheli) Link

Hyphæ creeping; conidiophores simple or more or less markedly dendritic branched, erect, branches various, thin and apically

pointed, thick and obtuse or cristate; conidia variously grouped at the apex of the branches, never in true heads, continuous, globose, elliptic or oblong, hyaline or light colored.

In part = *Sclerotinia*. See p. 101.

A genus of some two hundred or more species, several of them of great economic importance.

This form-genus contains many parasites on various hosts. In some instances they are known to include ascigerous stages, *Sclerotinia*, in their life cycle; in others no such relation is known, though it has often been assumed on quite untenable grounds. Specific limitations are but poorly understood and the relations between the various forms and between these forms and the ascigerous stages are in a state of much confusion (c. f. p. 101). In some instances the same conidial stage is claimed by different investigators as belonging to two distinct ascigerous species, a manifest impossibility, e. g., *S. fuckeliana* and *S. sclerotiorum* with *B. cinerea*.

The more prominent forms as described are given below, recognizing that some of them may be co-specific.

***B. cinerea* Pers.¹**

Hyphæ slender, constricted at septa, gregarious, simple or sparsely branched, erect, cinereous; conidia globose, pale.



FIG. 351.—*B. cinerea*.
After Smith.

On the lily, Ward, in a classic study demonstrated the parasitism of the fungus showing its action to be dependent upon toxins and enzymes. No ascigerous stage was found. The fungus has also often been reported on the cultivated geranium, dahlia, cyclamen, primrose.

On lettuce Humphrey, Jones, Bailey, and many others have reported a mold on the leaves due to a *Botrytis* which is often cited as *B. cinerea*. The affected part of the leaf collapses and is covered with a conspicuous growth of the conidiophores and conidia. On lemon trees it produces gummosis.

Other hosts are rose, various conifers, grape, *Prunus*, bean, horse chestnut, Douglass fir, pine, spruce, larch, hemlock.

On strawberries it penetrates all parts of the berry dissolving

¹ Brown, Wm. Studies in the physiology of parasitism. I. The action of *Botrytis cinerea*. *Ann. Bot.* **29**: 313, 1915.

the middle lamellæ and passing between the cells for considerable distance or penetrating the cell walls.

Numerous studies of the power of *B. cinerea* to infect growing tissue have been made with the conclusion that it is a weak parasite and that to become aggressively parasitic it must first develop a vigorous mycelium saprophytically. Attempts to immunize plants against its attack have been made with partial success.

***B. pœoniæ* Oud.**

Mycelium in the parenchyma of the host, hyphæ erect, 0.25–1 mm. high, protruding through the stomata, branches spirally arranged, simple or branched; conidia numerous in heads 12–15 μ across, oblong or ovate-oblong, 16–18 x 7–7.5 μ , hyaline or dilute colored.

It is reported as the cause of considerable injury to peonies in different parts of the United States. The greenish-black, flat sclerotia are found inside the stems.



Fig. 352.—*B. tulipæ*: a conidiophore with several clusters of conidia. After Hopkins.



FIG. 353.—*B. tulipæ*, showing attachment of the conidia to the conidiophores. After Hopkins.

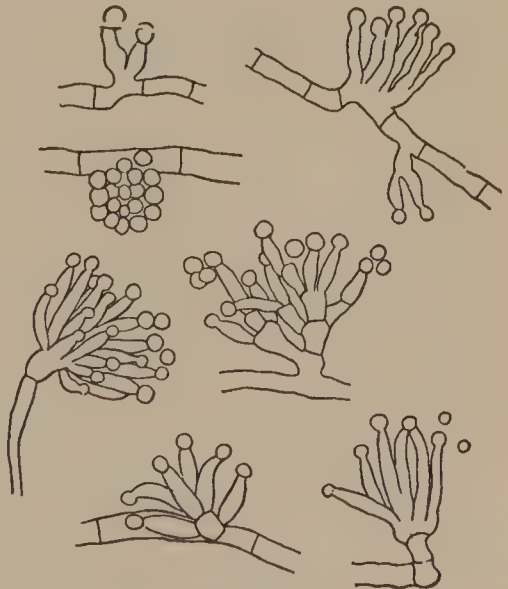


FIG. 354.—*B. tulipæ*, microconidia. After Hopkins.

B. tulipæ (Lib.) Hopkins.¹*B. parasitica* Cav.

Lesions occur on bulbs, leaves, petals and stalks of tulips. The mycelium is usually intercellular where it passes through the host tissue in advance of the death of the host cells, while in older parts of a lesion where the cells are dead it is intracellular. Though the cells are not killed immediately by the mycelium, evidences of disease are seen in advance of the mycelium indicating toxic or enzyme action. Infection occurs both with mycelium and with conidia without previous wound.

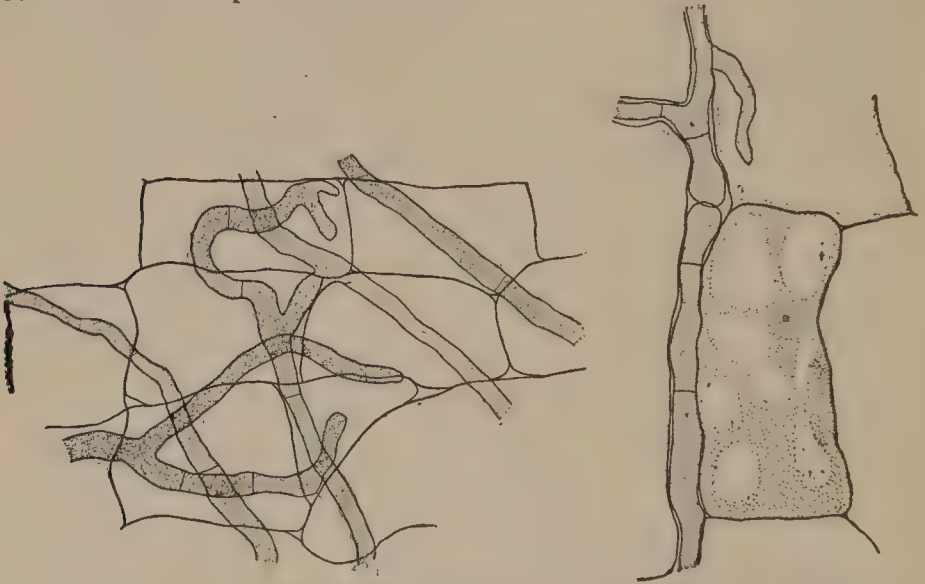


FIG. 355.—*B. tulipæ*, showing mycelium both inter- and intracellular. After Hopkins.

Mycelium variable in diameter, often anastomosing, branches not constricted at the base; conidiophores arising directly from the mycelium, erect, brown, proliferating, twisting on their axils when dry, slightly swollen at the base, dichotomous, apices swollen; conidia large, 12–24 x 10–20 μ , obovate, reddish brown in mass; microscopically gray to hyaline, smooth, with a short stalk, often or commonly not remaining attached; sclerotia at first white, finally black, small, 1–2 millimeters in diameter, circular or somewhat elliptical, flattened vertically and often convex; microconidia globose, about 3 μ in diameter, occurring on special, penicillate, obclavate conidiophores arising in white tufts from the substratum.

¹ Hopkins, E. F. The Botrytis blight of tulips. Cornell Agr. Exp. Sta. Mem. 45, 1921.

B. allii Munn

Conidiophores numerous, septate, erect, usually about 0.5 mm., high, occurring either singly or in clusters, not often branched on the host plant; conidia-bearing on upper portion, conidial clusters approximate; conidia hyaline or dilutely colored, elliptical, often slightly tapering at both ends, $7-16.2 \times 4-6 \mu$, attached by a short sterigma to the vesicles in small clusters; sclerotia dull-black, firm, white inside, flattened or concave below, strongly convex above; single sclerotia 1-5 mm. in diameter, usually several to many united in clusters or crusts which may be several centimeters in diameter. The sclerotia germinate by hyphæ which immediately produce conidiophores. No apothecia are produced.

Parasitic on leaves, flowers, and bulbs of onion.

Other reported hosts of Botrytis are Citrus, Prunus, raspberry, snowdrop, gooseberry, persimmon, egg-plant, lilac, lily-of-the-valley, carnation, dahlia, geranium, orchids, peony, primrose, golden seal, hemlock, horse-chestnut, larch, linden, pine, spruce, sycamore.

Ovularia Saccardo (p. 385)

Hyphæ simple or sparingly branched, erect, apically simple or dendritically branched; conidia globose or ovoid, solitary, rarely in short chains.

Over seventy-five species, all parasites.

O. canægricola Hen. is on economic species of Rumex.

O. armoraciæ Fel. on horse radish.

O. interstitialis B. & Br. and **O. primulana**

Thüm. on primrose leaves; **others** are on Vicia, primrose, alder, willow, lemons, lilac, alfalfa, clover.



FIG. 356.—Ovularia.
After Sorakin.

Verticillæ (p. 378)

Conidia acrogenous, on verticillate branches of the conidiophore.

KEY TO GENERA OF **Verticillæ**

Conidia solitary or loosely grouped, not in chains; conidia-bearing branches not very short; conidia globose to ovoid, tips of branches not in twos rectangularly; conidia not conglutinate, separating readily from the tips.

1. **Verticillium**, p. 390.

Conidia capitate, not in chains, sessile, involved in mucus, fertile hyphæ smooth.

2. **Acrostalagmus**, p. 390.

Verticillium Nees (p. 389)

Hyphæ creeping; conidiophores erect, verticillately branched; conidia borne singly at the apex of the branchlets, globose-ovoid, hyaline or light colored.

A form genus of some seventy-five species consisting in the main of conidia of various species of Hypocreales. See p. 145.

V. albo-atrum Reinke & Berthold.¹

Conidia ellipsoidal, unicellular, $4-11 \times 1.7-4.2 \mu$, cut off singly from the sterigma tips of verticillate conidiophores; primary whorls of branches, 1-8 in number, $30-90 \mu$ apart, sometimes bearing secondary verticils; branches 1-7, usually 3-5, in number, $13-38 \mu$ long, tapering, straight to slightly bowed; conidiophores $100-300 \mu$ or more in length. The terminal branch of the conidiophore is from $15-60 \mu$ long. Conidia may or may not be collected in heads on the sterigma tips. Mycelium septate, hyaline to brown with age, sometimes swollen into chlamydospore-like chains of closely septate, knotted masses. These constitute the sclerotia. It is a vascular parasite, the cause of a wilt of okra, potato, eggplant, cotton, snapdragon, and probably of species of Abutilon and Xanthium, ginseng, black raspberry, China aster, and dahlia.

On potato the vessels are browned into the tips of stems and into petioles.

Acrostalagmus Corda (p. 389)

Hyphæ creeping; conidiophores erect, septate, richly verticillately branched; conidia borne in slimy heads on the enlarged ends of the secondary branches.

Both of the fungi given below as in this genus may be identical with *Verticillium albo-atrum*.

A. albus Preu.

Hyphæ cespitose, effuse, slender, subangular, continuous or septate, conidiophores, $200-220 \times 1.7-2 \mu$, erect; fertile branches continuous, straight or curved; conidia in spherical heads, $9-10 \mu$

in diameter, numerous, minute, elliptic oblong, $3.3-3.4 \times 1-1.5 \mu$, hyaline.

¹ Carpenter, C. W. Wilt diseases of okra and the *Verticillium*-wilt problem. Jour. Agr. Res. **12**: 537, 1918.

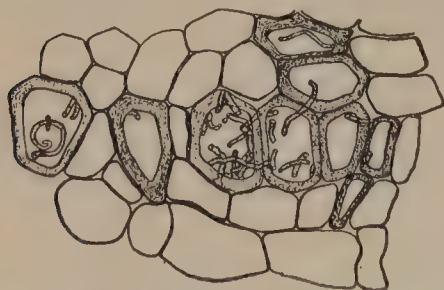


FIG. 357.—Cross-section of a vascular bundle. *Acrostalagmus* threads in the vessels. After Van Hook.

It causes a wilt of ginseng. The vascular bundles are yellowed and the ducts plugged by the mycelium. Entrance is apparently through the leaf scars.

A. caulophagus Law.

Tufts 1-3 mm. tall, forming long, floccose, irregular or short, thin, flaccid and arachnoid patches; conidiophores hyaline, 100-830 μ long, non-septate; laterals grouped or single, bearing one or two sets of numerous, short, simple, forked or whorled branches bearing heads of conidia; mycelium profusely septate, hyaline or olive-brown, 3-4 μ broad; chlamydospores spherical or oblong, single or in chains, 7-12 μ in diameter; heads of conidia hyaline, smooth, round 7.5-25 μ , bearing numerous conidia imbedded in a mucilaginous matrix that is readily soluble in water; conidia hyaline, oblong to oval, sometimes biguttulate, 3-7.5 x 2-3 μ . Parasitic in the stems of the black raspberry.



FIG. 358.—Spore-bearing stalks of *Acrostalagmus albus*. The spores are borne in heads and are held together at first by a coat of slime. After Van Hook.

Moniliaceæ-Didymosporeæ

Conidia hyaline or bright colored, 1-septate, ovoid oblong or short fusoid.

KEY TO GENERA OF Moniliaceæ-Didymosporeæ

Conidia not obliquely beaked.

Conidia smooth, capitate at apex of conidiophores

Fertile hyphæ simple..... 1. *Cephalothecium*, p. 392.

Fertile hyphæ dichotomously

branched, sterigmata subternate 2. *Cylindrocladium*, p. 392.

Conidia echinulate; conidial cells unequal.....

3. *Mycogone*, p. 392.

Conidia obliquely beaked.....

4. *Rhynchosporium*, p. 393.

Cephalothecium Corda (p. 391)

Hyphæ prostrate; conidiophores erect, simple, septate; conidia apical, subcapitate, oblong to pyriform, hyaline.

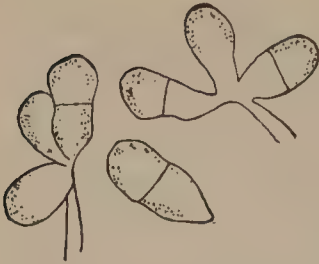
C. roseum Cda.

FIG. 359.—Spores of *Cephalothecium roseum*. After Eustace.

Cespitose in subrotund, rose colored spots, fading with age, byssoid; hyphæ creeping, branched; conidiophores erect, simple, continuous, hyaline; conidia oblong-ovate, constricted at the septum, capitate, light rose.

It is often found following apple scab gaining entrance through the injured cuticle and causing rot. A ring of pink conidiophores and conidia is formed around the margin of the scab.

Inoculation tests showed the fungus unable to penetrate through sound cuticle though it readily made entrance through wounds. It has been occasionally reported on living twigs and leaves.

Cylindrocladium Morgan
(p. 391)

Sterile mycelium creeping; fertile, erect, dichotomously or trichotomously branched; sterigmata on the tips of the branches in pairs or threes; conidia cylindrical, 1-septate, hyaline.

C. scoparium Morg.¹

Conidiophores see Fig. 360; conidia cylindrical, tapering, 1-septate, 40–50 x 4–5 μ . It causes canker on rose stems.

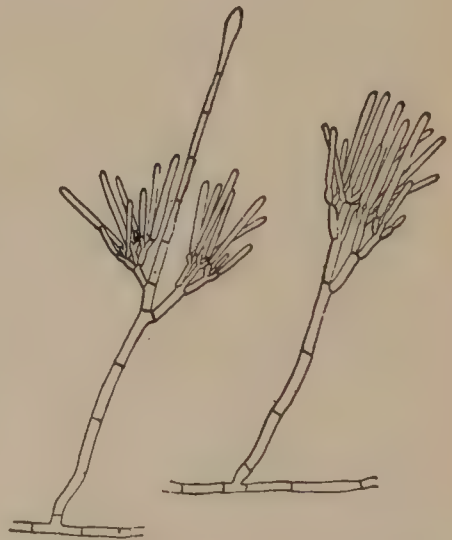


FIG. 360.—*C. scoparium*. conidiophores and conidia. After Anderson.

Mycogone Link (p. 391)

Hyphæ intricately branched; conidiophores short, lateral; conidia unequally 2-celled, the upper larger, echinulate.

¹ Anderson, P. J. Rose cancer and its control. Mass. (Amherst) Agr. Exp. Sta. Bul. 183, 1918.

There are about fifteen species of mycogenous fungi which are probably conidial stages of *Hypomyces*.

M. perniciosa Mag.

White throughout, byssoid, deforming the host; conidiophores short; conidia solitary, more or less pyriform, almost colorless, $17-22 \times 9-12 \mu$.

It is reported as the cause of a mushroom disease in America. A *Verticillium* conidial stage was present but no ascigerous form.

M. rosea Link also occurs on mushrooms.



FIG. 361. — *Mycogone*, conidiophores and conidia. After Saccardo.

Rhynchosporium Heinsen (p. 391)

On leaf spots; hyphæ filiform, hyaline, creeping, septate; conidiophores erect, with incurved branches, hyaline, apically denticulate; conidia short-cylindric, with short oblique beak, medially septate, hyaline.

R. secalis (Heins) Davis=*R. graminicola* Heins. This occurs on rye, wheat, and barley.

Spot oblong, 0.5–2 cm. long; conidia $13-19 \times 3.6 \mu$, hyaline, 1-septate.

Moniliaceæ-Phragmosporæ

Conidia hyaline or bright colored, 2 to several-septate, oblong, fusoid or elongate.

KEY TO GENERA OF **Moniliaceæ-Phragmosporæ**

- | | |
|---|-------------------------------------|
| Fertile hyphæ very short and little different from the conidia; conidia in chains, cylindric or oblong. | 1. Septocylindrium , p. 393. |
| Fertile hyphæ manifest and distinct from the conidia; conidia not mucose-conglobate | |
| Conidia ovate-cylindric or elongate, often catenulate. | 2. Ramularia , p. 394. |
| Conidia obclavate-pyriform. | 3. Piricularia , p. 395. |

Septocylindrium Bonordin

Conidiophores very short, scarcely distinct from the conidia or in parasitic species distinct but short and inflated or dentic-

ulately sublobate at the apex; conidia oblong or cylindrical, one to many-septate, catenulate, the chains often branched.

***S. areola* (Atk.) P. & C.**

Spots amphigenous, pale, becoming darker in age, 1–10 mm., angular, limited by the veins of the leaf, conidiophores amphig-

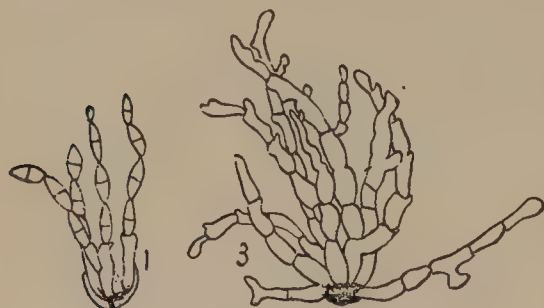


FIG. 362.—*S. areola*. After Atkinson.

enous, fasciculate, sub-nodose, branched or not, several times septate, hyaline, $25-75 \times 4-7 \mu$; conidia oblong, usually abruptly pointed at the ends, catenulate or not, $14-30 \times 4-5 \mu$, hyaline.

Leaf spots are produced on cotton. The conidia and stalks are so abundant on the

undersides of spots as to give them a frosted appearance.

***S. rufomaculans* (Pk.) P. & C.**

Spots numerous or confluent and even covering the entire leaf, reddish; conidiophores very short, hypophyllous, cespitose; conidia catenulate, variable, ellipsoid-oblong to cylindric, hyaline, $8-16 \times 3-4 \mu$.

It is somewhat injurious on buckwheat.

***Ramularia* Unger (p. 393)**

Conidiophores fasciculate, simple or with short, scattered branchlets, often flexuose, nodulose or denticulate towards the apex, hyaline or light colored; conidia acrogenous or acropleurogenous on the denticulations, hyaline, sometimes subcatenulate, oblong, cylindric, typically many-septate.

About three hundred species. In part = *Mycosphærella*. See p. 171.

***R. tulasnei* Sacc.** on strawberry = *Mycosphærella fragariæ*. See p. 171.

***R. armoraciæ* Fel.**

Spots amphigenous, subochraceous becoming gray; conidiophores fasciculate, continuous, subsimple, $40-50 \times 2.5-3 \mu$; conidia rod-shaped, obtuse, hyaline, $15-20 \times 3-4 \mu$.

On horse radish causing leaf spots.

Others are on dandelion, spinach, beet, ginseng, cacao, geranium, primrose, violet, *Heracleum*, sainfoin, artichoke, sweet potato, strawberry, *Narcissus*, coffee.

Piricularia Sacc (p. 393)

Conidiophores simple, rarely branched, conidia obelavate to pyriform, 2 to many-septate, solitary acrogenous, hyaline.

A small genus of parasites.

P. grisea (Cke.) Sacc. produces pallid or water-soaked spots on culms and leaves, with age grayish; conidiophores in clusters of two or five from the stomata, simple or rarely sparingly branched, grayish, septate; conidia single, terminal in scorpioid cymes, ovate, 2-septate, $24\text{--}29 \times 10\text{--}12 \mu$.

It causes death of rice plant tissue and the disease called "blast." If affected leaves or stalks are placed in a damp atmosphere, for about a day a delicate grayish fungus, the sporing mycelium, appears. The fungus grows well in culture and applied to the rice plants gives rise to the typical disease spots. It also occurs on millet.

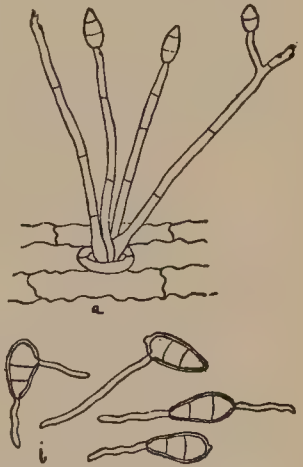


FIG. 363.—*Piricularia grisea*. a, conidiophores. i, germinating spores. After Fulton.

Moniliaceæ-Scolecosporæ

Cercospora Saccardo

Hyaline throughout; conidiophores simple or branched; conidia filiform, many-septate. Distinguished from *Cercospora* only in color. The genus contains some seventy species of parasites.

C. persicæ Sacc.

Conidiophores cespitose, on discolored areas, filiform, 2 to 3-branched, continuous; conidia $40\text{--}60 \times 1\text{--}5 \mu$, torulose.

The conidia develop in abundance on the lower sides of leaf spots of peach causing a frosty mildew.

Others are on *Narcissus*, lily, parsnip and other Umbelliferæ, and on turnip.



FIG. 364.—*C. persicæ*. After Saccardo.

Dematiaceæ (p. 377)

Hyphæ dark or black, cobwebby, loose, usually rigid, not cohering in definite fascicles; conidia typically dark and concolorous, but sometimes the hyphæ are dark and conidia clear, or the conidia dark and the hyphæ clear. This family parallels the Moniliaceæ and certain intermediate forms must be sought in both.

Dematiaceæ-Amerosporæ

Conidia continuous, globose to oblong.

KEY TO SUBFAMILIES OF Dematiaceæ-Amerosporæ

Conidiophores very short, scarcely distinguishable from the mycelium

Conidia catenulate..... 1. **Toruleæ**, p. 396.

Conidiophores manifest and distinct from the mycelium and spores

Conidia dark, rarely subhyaline, in chains 2. **Haplographieæ**, p. 397.

Toruleæ

Conidia in chains.

KEY TO GENERA OF Toruleæ

Conidia of two sorts, microconidia internal, catenulate.....

1. **Thielaviopsis**, p. 396.

Conidia all alike; hyphæ hyaline.....

2. **Monilochætes**, p. 397.

Thielaviopsis Went.

Hyphæ creeping, subhyaline; conidiophores simple, septate; conidia of two kinds; macroconidia catenulate, ovate, fuscous; microconidia cylindric, hyaline, catenulate within the conidiophore. In part=*Trichosphæria*.

T. paradoxa (d. Seyn) v. Höhn (= *Chalara paradoxa*)

Macroconidia 16–19 x 10–12 μ ; microconidia 10–15 x 3.5–5 μ .

It is the cause of a pineapple rot and of a sugar-cane disease.

In addition to micro and macrospores the fungus possesses a pycnidial form. With variation of the substratum the spores vary considerably from the typical.



FIG. 365. — *T. ethacetica*.
After Wakker and Went.

Monilochaëtes Ell. & Hals. (p. 396)

Hyphæ dark, erect, rigid, septate, not in definite fascicles; conidia distinctly different from the sporophores and hyphæ, hyaline, slightly brown with age, continuous, not in chains, acrogenous.

M. infuscans Ell. & Hals.¹

On the host definite vegetative hyphæ are lacking; sporophores septate, erect, unbranched, dark, and attached to the host singly

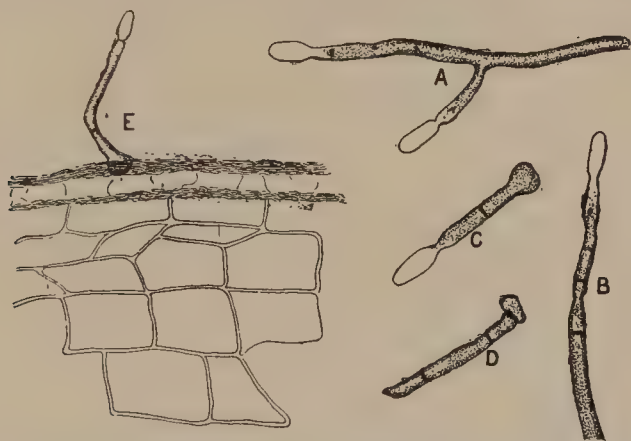


FIG. 366.—*M. infuscans*. *A*, a branched conidiophore with conidia attached. *C*, a conidiophore from host, with conidium attached. *B*, an unbranched conidiophore, showing septation; conidium attached. *D*, a conidiophore from the host, showing the peculiar basal cell and septation. *E*, a conidiophore from the host, showing diagrammatically the attachment to the host by a bulblike enlargement of the basal cell. After Harter.

or by twos, by a bulblike enlargement, $40\text{--}175 \times 4\text{--}6 \mu$, bearing rarely a hyaline, one-celled, oblong spore; conidia 1-celled, hyaline, ovoid to oblong, $12\text{--}20 \times 4\text{--}7 \mu$, solitary, terminal.

The causes of scurf disease of sweet potatoes.

Haplographieæ (p. 396)

Conidia dark, catenulate.

Hormodendrum Bonorden

Hyphæ creeping; conidiophores erect, septate, brown, variously dendritically branched; conidia catenulate on the branches, globose, ovoid, olivaceous to fuscous.

¹ Harter, L. L. Sweet-potato scurf. Jour. Agr. Res. **5**: 791, 1916.



FIG. 367.—*H. hordei*.
After Bruhne.

H. hordei Bruhne on barley stems and leaves often reduces the yield.

Spots brown, scattered over the entire leaf or confluent, oblong; hyphæ simple, septate; conidia various, cylindric, rounded or subattenuate, or ellipsoid to subglobose, verrucose.

Dematiaceæ-Didymosporæ

Conidia 2-celled, dark, rarely hyaline, ovoid or oblong.

KEY TO GENERA OF Dematiaceæ-Didymosporæ

Hyphæ very short or scarcely different from the conidia

Conidia not in chains..... 1. *Cycloconium*, p. 398.

Hyphæ distinctly different from the conidia;
conidia smooth, muticate, not
capitate

Conidia more or less catenulate at
first

Hyphæ and conidia uniform, in-
flated, somewhat decumbent;
conidia short-catenulate or fi-
nally solitary..... 2. *Cladosporium*, p. 399.

Conidia not catenulate

Hyphæ flexuose-torulose..... 3. *Polythrincium*, p. 401.

Hyphæ not torulose or flexuose,
not inflated, usually short and
little branched

Conidia acrogenous; conidio-
phores short, 1 or 2-septate 4. *Fusicladium*, p. 401.

Conidia acro-pleurogenous.... 5. *Scolecotrichum*, p. 402.

Cycloconium Castaigne

Hyphæ in the walls of the epidermis, dichotomous branched, very fugacious, black; conidia ovoid, solitary.

C. oleaginum Cast. Mycelium circinate, fugacious, black; conidia sessile, ovoid, yellow-green.

It forms blotches on olive leaves and on peduncles of the fruit.

Cladosporium Link (p. 398)

Hyphæ decumbent, intricately-branched, olivaceous; conidia globose to ovoid, greenish. In part = *Mycosphærella*. See p. 171.

Some one hundred seventy-five species, many of them of economic importance.

C. herbarum (Pers.) Lk. on many hosts = *Mycosphærella tulasnei*. See p. 175.

C. citri Mas.¹

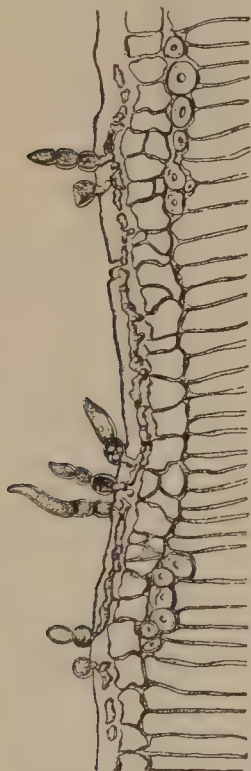


FIG. 368.—*Cycloconium oleaginum*. After Boyer.



FIG. 369.—*Cladosporium cucumerinum*, mycelium, a hyphal knot, conidiophore and spores. After Humphrey.

The fungus that causes scab on lemons, sour oranges, satsumas and pomelos, usually referred to under this name, does not belong to this genus, but apparently does belong to the Dematiaceæ-Amerosporæ.

C. herbarum (Pers.) Lk. var. *citricolum* Fawcett causes scaly

¹ Winston, J. R. Citrus scab: its cause and control. U. S. Dept. Agr. Bull. 1118, 1923.

bark of Citrus. The fungus was grown in pure culture and inoculations were made resulting in from forty to sixty days in typical spots.

C. cucumerinum E. & A.

Effused, maculose, in mass grayish-brown, changing to dark olivaceous, forming spots on fruits; conidiophores cespitose, sparingly septate, simple, denticulate, pale; conidia ovoid, lemon-shaped or fusoid; olivaceous, $10-13 \times 3-4 \mu$. It causes watery spots on cucumber leaves, also decayed spots in fruit.



FIG. 370.—*C. carpophilum*. After Cobb.

C. carpophilum Thüm.

Spots orbicular, often confluent, blackish-green, forming circles; conidiophores erect, simple, sinuous, septate; conidia ovate, obtuse, continuous or 1-septate, $10-12 \times 4-6 \mu$.

Widely distributed causing scab of peach, plum, nectarine, apricot, cherry.

In the twig the fungus breaks the cuticle from the layers below and its hyphæ project through cracks. Upon the leaf it causes shot holes.

C. fulvum Cke.

Conidiophores densely crowded rupturing the cuticle, sparingly branched, septate, nodulose, bearing a few conidia near the apex;

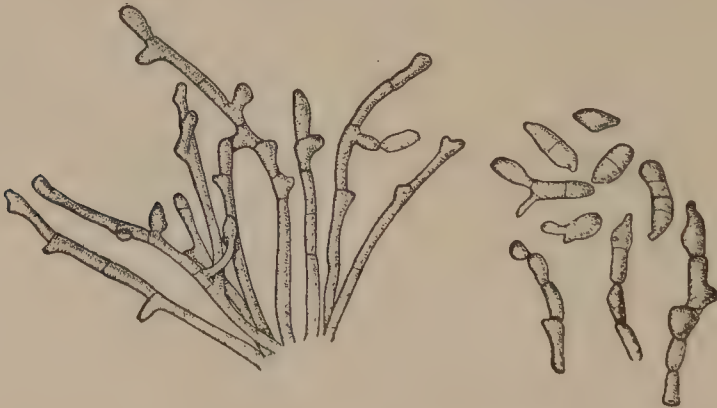


FIG. 371.—*C. fulvum*. After Southworth.

conidia elliptic-oblong, 1-septate, translucent, tawny, $10-20 \times 4-6 \mu$.

The hyphæ are abundant on the lower sides of tomato leaves, forming a mold, varying from whitish to purplish in color.

C. macrocarpum Preù.

Subeffuse, black; conidiophores subfasciculate, simple, some-

what flexuose, brown; conidia oblong, or oblong-ovate, 2 to several septate, obtuse, pale brown.

On spinach leaves causing disease.

Others are on grape, cranberry, sweet potato, tomato, cucumber, corn, rice, pea, peony, *Oncidium*, oak, sycamore, poplar, walnut, beech, elm.

Polythrincium Kunze & Schmidt (p. 398)

Conidiophores erect, fasciculate, regularly flexuose or torulose, black, simple; conidia acrogenous, obovoid.

P. trifolii Kze. on clover has been said to be the conidial stage of *Phyllachora trifolii*.

Fusicladium Bonorden (p. 398)

Conidiophores short, erect, straight, sparingly septate, subfasciculate, olivaceous; conidia ovoid or subclavate, continuous or 1-septate, acrogenous, solitary or paired.

In part = *Venturia* and *Phyllachora*.

Over forty species, several pathogenic.

F. fraxini Aderh. on Ash. = *V. fraxini*.

F. saliciperdu (All. & Pub.) Lind. on *Salix* = *V. chlorospora*.

F. cerasi (Rab.) Sacc. on cherry, peach, = *V. cerasi*.

F. pirinum (Lib.) Fel. on pear = *V. pirina*. See p. 182.

F. dendriticum (Wal.) Fel. on pomaceous fruits = *V. inæqualis*.

See p. 182.

F. orbiculatum Thüm on *Sorbus* = *V. inæqualis* var. *cinerascens*.

F. depressum (B. & Br.) Sacc. on *Umbelliferæ* = *Phyllachora*.

F. betulæ Aderh. on birch = *V. ditricha*.

F. tremulæ Fr. on aspen = *V. tremulæ*.

F. destruens Pk.

Conidiophores short, 20–50 μ , fasciculate, continuous or 1 to 2-septate, basally, colored, clusters slightly olive-green; conidia acrogenous, continuous or 1-septate, subcatenulate, ellipsoid to oblong, colored, 7–20 x 5–7 μ .

On oats.

F. effusum Wint.

Spots minute, rounded, rarely effused, confluent, smoky; conidiophores erect, simple or slightly branched, septate, torulose, brownish, lighter above, 100–140 x 4 μ ; conidia oblong fusoid to

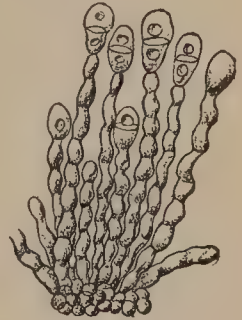


FIG. 372.—*P. trifolii*. After Corda.

rhomboid, continuous or uniseptate, light fuscous, subtruncate, 17–24 x 5.5–7 μ .

It constitutes the pecan scab, affecting the leaves, stems and nuts.

Others are on buckwheat, flax, *Eriobotrys*.

Scolecotrichum Kunze & Schmidt (p. 398)

Conidiophores short, subfasciculate, olive; conidia oblong or ovate, pleurogenous or acrogenous.

A genus of some thirty species very similar to *Fusicladium*.

S. graminis Fcl.

Spots foliicolous, elongate, ochraceous; conidiophores densely fasciculate, filiform, simple, sinuous, 90–100 x 6–8 μ , subcontinuous; conidia fusoid-obclavate, 35–45 x 8–10 μ , uniseptate, olive-brown.

It is common, causing leaf spots on grasses, especially on *Avena* and *Phleum*. The mycelium collects below the stomata and pushes its tuft of hyphæ through them.

Others are on ash, Iris, banana, oats.



FIG. 373.—*S. graminis*.
After Saccardo.

Dematiaceæ-Phragmosporæ

Conidia 2 to many-celled, dark, rarely light or hyaline, ovoid to cylindric or vermicular.

KEY TO GENERA OF **Dematiaceæ-Phragmosporæ**

Fertile hyphæ very short or little different from the conidia

Conidia not in chains, muticate; straight ovoid to cylindric, solitary 1. **Clasterosporium**, p. 403.

Fertile hyphæ distinctly different from the conidia

Conidia solitary or nearly so, acrogenous for the most part

Conidia echinulate 2. **Heterosporium**, p. 403.

Conidia smooth

Hyphæ short, ascending or erect, conidia ovoid to oblong 3. **Napicladium**, p. 404.

- Hyphæ longer, rigid; conidia elongate,..... 4. **Helminthosporium**, p. 404.
 Conidia verticillate, pleurogenous; hyphæ dark, not rostrate at apex. . 5. **Spondylocladium**, p. 407.

Clasterosporium Schweinitz (p. 402)

Hyphæ creeping, here and there swollen, conidiophores erect, bearing 2 to several-septate, solitary, apical conidia.

A genus of some seventy-five species.

C. carpophilum (Lév.) Aderh. Aderhold by inoculations, properly controlled, showed this fungus capable of causing gummosis of prunaceous hosts.

Effuse, hyphæ simple or short-branched, densely aggregated, septate, conidia elongate-fusoid, obtuse, 4 to 5-septate, slightly constricted at the septa. It is commonly seen as the cause of a brown spot on peaches. Spores do not appear in the young spots but are found sparingly in older brown areas.

C. amygdalearum (Pass.) Sacc. is also described on rosaceous hosts. It is perhaps identical with *C. carpophilum* and may be connected with *Pleospora vulgaris*.

C. putrefaciens (Fel.) Sacc. causes spots on leaves of the sugar-beet.

Heterosporium Klotzsch (p. 402)

Hyphæ subcespitose, smoothish, often branched; conidia oblong, 2 to several-septate, smoothish to granular or echinulate.

A genus of forty species or more.

H. echinulatum (Berk.) Cke.

Spots gregarious, on fuscous areas; conidiophores fasciculate from a stromatic base, 150–200 x 8 μ , rarely shorter, flexuose-nodose, fuliginous; conidia at the nodes, oblong-cylindric, rounded at the ends, 2 to 3-septate, 40–50 x 15–16 μ , slightly constricted, roughened, brownish.

It causes a destructive mold on carnation leaves and stems.

H. variable Cke.

Conidiophores flexuose, slender, more or less nodulose at the septa; conidia cylindric oblong, 2 to 4-septate, minutely warted, 20–25 x 7–10 μ , pale olive. On spinach.

Other parasitic species are on Liliaceæ, larch, *Auricula*, lilac, hop, Iris, Narcissus and other Monocotyledons.

Napicladium von Thümen (p. 402)

Conidiophores short, subfasciculate, smoothish; conidia acrogenous, solitary, large, oblong, 2 to many-septate, smoothish.

A small genus.

N. soraueri is a form of *Venturia inæqualis* with somewhat atypical napiform spores.

N. janseanum Rac. is on rice.

Helminthosporium Link (p. 403)

Conidiophores erect, rigid, subsimple, fuscous; conidia fusoid to elongate-clavate or cylindric, pluriseptate, fuscous, smooth.

In part=*Pleospora*. See p. 188.

About two hundred-fifty species; several are important pathogens, others saprophytes.

The species show biologic differentiation into races similar to that exhibited in the *Erysiphaceæ*, though morphologically they may be inseparable.

Saltation¹ has also been shown to occur commonly in the genus and definite determination of species is extremely difficult. The conidial forms named below have been considered responsible for diseases on the hosts mentioned in connection with them.

H. gramineum Rab. on grasses=*Pleospora gramineum*. See p. 189.

On barley it causes the leaf-stripe disease.

The conidiospores have been shown to be long-lived and spring infection begins largely from conidia carried over winter on the seed. The mycelium invades the tissue causing long brown spots. These later bear conidiophores. Ravn regards the disease produced by *H. gramineum* as often general, not local, in that the mycelium invades the embryonic tissue of the growing points, resulting in infection of all the leaves.

H. trichostoma=*Pleospora trichostoma*. See p. 189.

H. teres Sacc.

On barley causing net blotch. Spots oblong.

The hyphæ, according to Ravn, penetrate the outer cell wall of the epidermis then branch abundantly and may fill the cell

¹Stevens, F. L. The *Helminthosporium* foot-rot of wheat, with observations on the morphology of *Helminthosporium* and on the occurrence of saltation in the genus. Ill. Nat. Hist. Surv. Bulletin, **14**: Art. 5, 77, 1922.

completely; they then proceed into the intercellular spaces of the mesophyll and thereafter remain intercellular.

H. avenæ-sativæ (B. & Cav.) Lind.

On oats causing leaf spots.

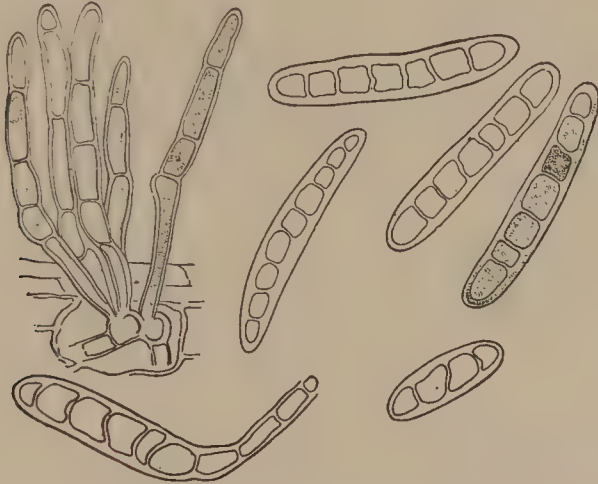


FIG. 374.—*Helminthosporium gramineum*. Conidiophores and spores. After King.

The conidia of the last two species infect grains and seedlings. The conidia spread the disease from the early infection centers to other parts of the plants but the mycelium remains local.

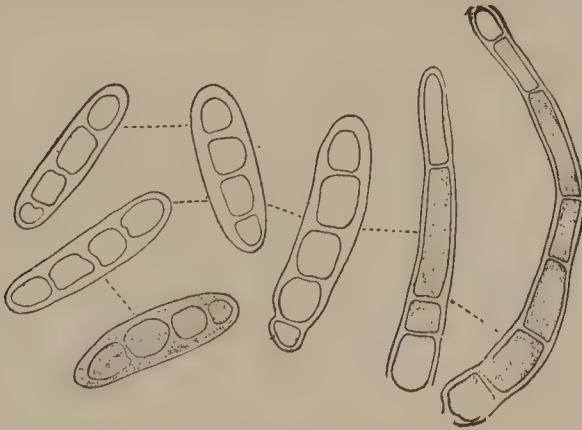


FIG. 375.—*Helminthosporium teres*. Conidiophores and spores. After King.

H. bromi Died. on *Bromus*=*Pleospora bromi*, see p. 189.

H. tritici-repentis Died.=*Pleospora tritici-repentis*, see p. 189.

H. sativum Pamm., King & Bakke

The cause of a destructive late blight, spot blotch, of barley. The disease manifests itself by dark colored, elongate spots on



FIG. 376.—Showing variation in conidial shape and septation of H. No. 1, also the dark spot, stipe, at basal end, and the pale apical spot. After Stevens.

the leaves. It also occurs on the glumes and spikelets, sometimes even penetrating the grains.

A member of the *H. sativum* group is the cause of rotting of the basal part of the stems of wheat (foot rot) also of rye. The particular strain (Stevens H. No. 1) causing this rot of wheat is characterized by a conidium with a very short, $2 \times 4 \mu$, black stipe at the base (Fig. 376) and with a pale spot at the apex. The conidia are from 4 to 10-septate, (mode 8), their length $34-99 \mu$, (mode 78μ) their thickness $17-24 \mu$ (mode 20μ).

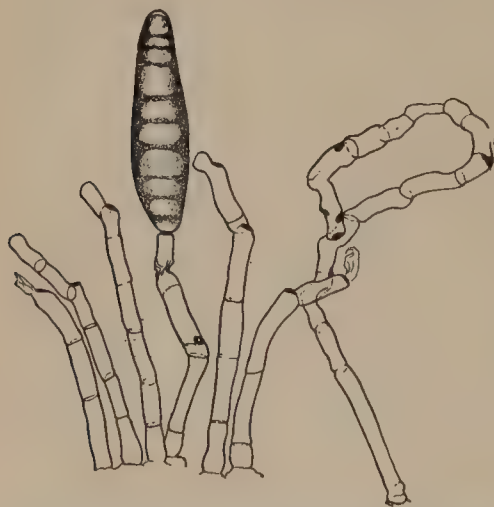


FIG. 377.—H. No. 1, showing variation in conidiophores, geniculation, conidia-scars, and septation. After Stevens.

Infection is directly through the cuticle, not stomatal, and the mycelium is intercellular within the host.

H. sorokinianum Sacc. is reported on wheat and rye.

H. turcicum Pass.

Spots, large, dry, brownish; conidiophores, gregarious to fascicu-

late, septate, $150-180 \times 6-9 \mu$, pale olive, apex almost hyaline, often nodulose; conidia spindle-shaped, acute, 5 to 8-septate, pale olive, $80-140 \times 20-26 \mu$.

It produces spots on corn and sorghum.

H. inconspicuum C. & E.

Conidiophores elongate, septate, nodose, pale brown; conidia lanceolate, 3 to 5-septate, $80-120 \times 20 \mu$, smooth.

On corn and oats.

H. inaequalis Shear

Sterile hyphae effuse, much branched, dark brown; conidiophores erect, septate, variable in length, $6-8 \mu$ in diameter; conidia both terminal and lateral, more or less curved, 3 to 5-celled, thick-walled, brown, $23-32 \times 11-14 \mu$. On cranberry.



FIG. 378.—*Helminthosporium inaequalis*. After Shear.



FIG. 379.—*S. atrovirens*, a conidiophore and conidia from mycelium in a potato cell. After Appel and Lambert.

Spondylocladium Martius (p. 403)

The genus is characterized by its dark, multiseptate conidiophores, which bear the many-celled conidia pleurogenously in the form of whorls.

S. atrovirens Harz ¹

The conidia are formed first either at the apex or the distal end of the intermediate cells. The lowest whorls of the conidia are borne about halfway between the base and the apex of the conidiophores, and the conidia are attached at the broad end. They vary in length from $18-64 \mu$, in breadth from $6-12 \mu$, and are 4 to 8-septate. It is the cause of potato silver-scurf. The fungus enters the tuber through the lenticels or directly through the epidermis and is limited to the corky layer, resulting in sloughing off of the corky and epidermal layers.

¹ Schultz, Eugene S. Silver-scurf of the Irish potato caused by *Spondylocladium atrovirens*. Jour. Agr. Res. 6: 339, 1916.

Dematiaceæ-Dictyosporæ

Conidia dark, rarely light muriform, globose to oblong.

KEY TO GENERA OF Dematiaceæ-Dictyosporæ

- Hyphæ very short or scarcely different from the conidia..... I. **Micronemeæ**.
 Conidia not in chains, not appendaged, irregularly muriform or sarciniform, without conic points, ovoid to oblong, loose..... 1. **Sporodesmium**, p. . 408
 Hyphæ distinctly different from the conidia II. **Macronemeæ**.
 Conidia uniform
 Conidia not in chains or capitate
 Conidia single
 Hyphæ alike; conidia muriform, typically smooth
 Hyphæ decumbent..... 2. **Stemphylium**, p. 408.
 Hyphæ erect or ascending
 Conidia ovoid to oblong, acrogenous; conidiophores somewhat lax, colored..... 3. **Macrosporium**, p. 409.
 Conidia catenulate; hyphæ velvety, erect, subsimple; conidia caudate.. 4. **Alternaria**, p. 410.

Sporodesmium Link

Mycelium and conidiophores poorly developed; conidia ovoid oblong, subsessile or short-stalked, rather large, clathrate-septate, fuliginous.

S. piriforme Cda..on oranges=*Pleospora hesperidearum*.

S. exitiosum Kühn on crucifers=*Leptosphaeria napi*.

Others are on potato, cucumber, salsify, egg-plant, asparagus, beet.

Stemphylium Walroth

Conidiophores decumbent, intricately branched, hyaline or smoky; conidia acrogenous, ovoid to subglobose, 2 to many-muriform-septate, fuliginous.



FIG. 380.—*Sporodesmium anti-quum*. After Saccardo.

S. cucurbitearum Osner¹

Sporophores arise singly on the lower surface of the leaf, hyaline to light brown, 1 to 5-septate, $10-30 \times 7-12 \mu$, the individual cells becoming globose and easily broken apart, bearing a single spore at the apex; the spores are nearly globose, dark brown, muriform, $25-50 \mu$ in diameter, composed of 5-20 cells each of which is $10-18 \mu$ in diameter, easily breaking away from the sporophores. On leaves, stems, and petioles of gourds, cucumber and squash causing leaf spots.

S. citri Pat. & Charles

Vegetative mycelium long, hyaline, becoming dark, 4μ in diameter, septate; conidiophores short; conidia dark brown, subglobose to oblong, apiculate, irregularly muriform, $20-30 \times 12-15 \mu$, usually in chains of three.

This is found associated with an end-rot of oranges and is perhaps the cause of the disease.

S. tritici Pat.

Hyphæ irregularly branched; conidiophores closely septate, $4-5 \mu$ in diameter; conidia catenulate, irregular, usually clavate, constricted slightly at the septa, $24-35 \times 12-15 \mu$, vermiculate, fuliginous, isthmus short, $3-4 \mu$ in diameter. It is described as the cause of floret sterility of wheat.



FIG. 381.—*Stemphylium*.
After Saccardo.

Macrosporium Fries (p. 409)

Conidiophores fasciculate, erect or not, more or less branched, colored; conidia usually apical, not catenulate, elongate or globose, dark-colored.

In part= *Pleospora*. See p. 188.

Macrosporium is distinguished from *Alternaria* by its solitary spores, not catenulate. Elliott² believed catenulation in these forms to be correlated with an attenuated apex, therefore that all beaked spores of the *Alternaria*-*Macrosporium* type, under suitable conditions, would produce chains. Applying this distinc-

¹ Osner, George A. *Stemphylium* leafspot of cucumbers. Jour. Agr. Res. **13**: 295, 1918.

² Elliott, J. A. Taxonomic characters of the genera *Alternaria* and *Macrosporium*. Am. Jour. Bot. **4**: 439, 1917.

tion most of the forms previously reported as *Macrosporium* would be regarded as *Alternarias*.

M. commune Rab.=*M. sarcinula parasiticum* Thüm. on various grasses=*Pleospora herbarum*.

It is reported as the common black mold which follows *Peronospora* on the onion and which occurs often also on onions not so diseased, being especially common on the seed stalks. It is usually associated with injured plants and may be important only as a wound parasite.

M. porri E., **M. alliorum** C. & M. and **M. sarcinula** Berk. are also on onion.

Others are reported as causing disease on cantaloupe, grape, pepper, rice, turnip, horseradish, cabbage, collards, and other crucifers, celery, tobacco, red clover, cotton, lettuce, iris, *Chieranthus*, violet, *Saponaria*, geranium, catalpa, hackberry.

Alternaria Nees. (p. 408)

Conidiophores fasciculate, erect, subsimple, short; conidia clavate-lageniform, septate, muriform, catenulate.

In part=*Pleospora*. See p. 188.

A. sp. on *Tropæolum*=*Pleospora tropæoli*.

A. trichostoma Died. on barley=*Pleospora trichostoma*. See p. 189.

A. brassicæ (Berk.) Sacc.

Conidiophores short, continuous, short-branched, apically equal; conidia elongate, fusoid, clavate, 60–80 x 14–18 μ , 6 to 8-muriform-septate, olivaceous. On crucifers generally.

A. brassicæ (Berk.) Sacc. var. **nigrescens**

Pure cultures have been obtained and successful inoculations made on normal uninjured melon leaves.

It is also reported as the probable cause of muskmelon leaf spots.

A. violæ G. & D.

Conidiophores erect, pale-olive, septate, simple, 25–30 x 4 μ ; conidia in chains at or near the apex of the conidiophore, clavately flask-shaped, strongly constricted at the septa, olive, 40–60 x 10–17 μ .

Circular leaf spots are produced on violets. Spores are found on the spots only when conditions are most favorable, i. e., in a humid air. The parasitism of the fungus was demonstrated by inoculation with spores on living leaves in distilled water.

A. citri Pierce ¹ is held to be responsible for the abscissions resulting in the June drop of Navel oranges also of a black rot of the fruits.



FIG. 382.—*A. violæ*, germinating spores. After Dorsett.

A. dianthi S. & H.

Spots epiphyllous, ashen-white, definite, circular. Conidiophores



FIG. 383.—*A. dianthi*. 3, Mycelium showing branching and septation. 4, Showing mycelium below stoma and hyphæ emerging through the stoma. 5, Showing catenulate spores as borne upon hyphæ. 6, Spores showing shape, septation and catenulation. 7, A young cluster of hyphæ. 8, An older cluster of hyphæ. After Stevens and Hall.

cespitose from stomata, amphigenous, dark-brown, 1 to 4-septate, erect, 1–25 from a stoma; conidia 26–123 x 10–20 μ , clavate,

¹ Coit, J. Eliot and Hodgson, Robert W. An investigation of the Abnormal Shedding of Young Fruits of the Washington Navel Orange. Univ. of Cal. Pub. Agr. Sci. 3: 283, 1919.

tapering, obtuse, basally dark-brown, slightly constricted at the septa, 5 to 9 times cross-septate and 0-5 times longitudinally septate.

It causes injury on carnation leaves and stems.

A. solani (E. & M.) Jones & Grout

Spots brown, circular to elliptic, concentrically zonate, amphigenous, irregularly scattered over the leaf surface; mycelium, light-brown; conidiophores erect, septate, 50-90 x 8-9 μ ; conidia ob-

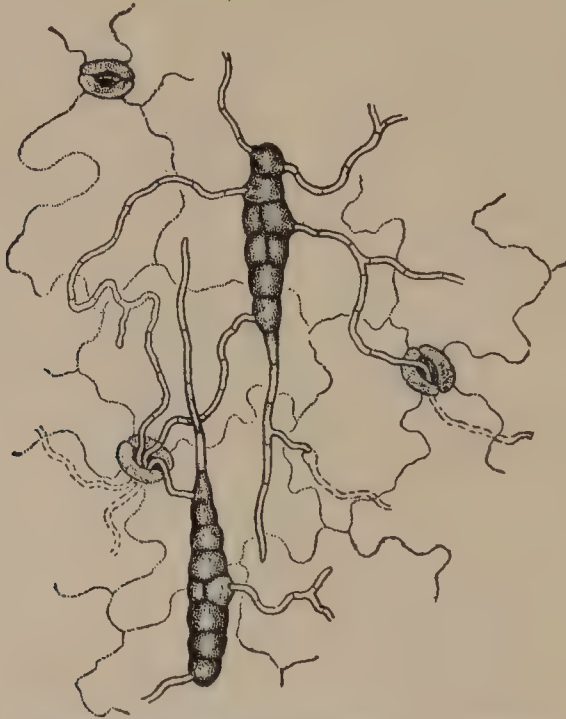


FIG. 384.—*A. solani*, spores germinating and penetrating the living potato leaf. After Jones.

clavate, brown, 145-370 x 16-18 μ with 5 to 10 transverse septa, longitudinal septa few, conidia terminating in a very long, hyaline, septate beak half the length of the conidium or longer.

It causes early blight, a leaf spot disease of potatoes and tomatoes. Its pathogenicity was proved by inoculations on tomato and potato, the spots appeared in eight to ten days after inoculation on vigorous uninjured leaves. The mycelium grows luxuriantly within the leaf but spores do not usually form until after the death of the supporting tissues when the conidiophores emerge

through the stomata or by rupturing the epidermis. Often no spores are formed and rarely are many present. The mycelium may live a year or more and resume sporulation the following season.

A. fasciculata (C. & E.) Jones & Grout

Conidiophores light or dark-brown, becoming almost black, darker than the vegetative hyphæ, but like them echinulate, $30-40 \times 4-5 \mu$; conidia concolorous with the conidiophores, $35-66 \times 16-20 \mu$, obclavate, 3 to 6 times cross-septate, 1 to 2 longitudinal septa, apical cell hyaline.

This fungus is associated as a saprophyte with the blossom-end-rot of tomatoes and also causes a serious decay of the ripened fruit. The literature of the disease is rather voluminous and contains a number of synonyms, among them *Macrosporium* tomato, *M. lycopersici*, *M. rugosa*, *M. fasciculata*.

A. mali Roberts enlarges dead spots of apple leaves; another species causes core rot. **Others** are on Forsythia, carrot, tobacco, ginseng, fig, grape, olive.

Dematiaceæ-Scolecosporæ

Conidia dark or subhyaline, vermiform or filamentous, multiseptate.

There is only one genus.

Cercospora Fries.

Conidiophores variable, almost obsolete or well developed, simple or branched; conidia vermiform or filiform, straight or curved, multiseptate, subhyaline to dark.

In part=*Mycosphærella*. See p. 171.

The genus is a very large one, some seven hundred species, and contains very many aggressive, important parasites, chiefly causing leaf spotting. The spots are often blached and are rendered ashen colored in the centers by the presence of the dark hyphæ. The hyphæ are usually geniculate at the point of spore production, Fig. 388, and thus old hyphæ bear traces of spores previously borne.

C. cerasella Sacc. on cherries=*Mycosphærella cerasella*. See p. 172.

C. gossypina Cke. on cotton = *Mycosphærella gossypina*. See p. 176.

C. circumscissa Sacc.

Spots amphigenous, circular, pallid, dry, deciduous; conidiophores fasciculate, nodulose, brownish, simple; conidia acicular, narrowed apically, attenuate, tinged brown, $50 \times 3.5\text{--}4\ \mu$.

On various species of *Prunus* this causes leaf holes.

It is reported as especially serious on the almond.

C. angulata Wint.

Spots roundish, angulate, whitish to cinereous, margined, 1–3 mm. in diameter, often confluent; conidiophores hypophyllous, fasciculate, erect, straight or only slightly flexuose, simple, brownish, few-septate, $78\text{--}105 \times 5\ \mu$; conidia filiform-obclavate, long attenuate, hyaline, 7 to 16-septate, $80\text{--}170 \times 3.5\ \mu$.

On the currant.

C. concors (Casp.) Sacc.

Spots amphigenous, pale above, whitish beneath, rounded, indefinite; conidiophores fasciculate or single from the stomata, erect, brown, septate, simple, $40\text{--}80\ \mu$ high; conidia single, apically variable in form, ovate to elongate, curved, 1 to 5-septate, subhyaline, $15\text{--}90 \times 4\text{--}6\ \mu$.



FIG. 385.—*C. concors*. Hyphae emerging through a stoma and twining about a hair. After Jones and Pomeroy.

Conidia are abundant on the spots, on potato leaves, on stalks emerging from the stomata. The superior and inferior hyphae differ considerably in length and branching. Brown beadlike chlamydospores form within the leaf. The mycelium is strictly intercellular. Inoculations result in disease spots in about three weeks after spraying with suspensions of spores.

C. nicotianæ E. & E.

Spots amphigenous, pale, becoming white, with a narrow and inconspicuous reddish border, 2–5 mm. in diameter, conidiophores amphigenous, tufted, brown, septate, 2 or 3-times geniculate above, simple or sparingly branched, septate, $75\text{--}100 \times 4\text{--}5\ \mu$; conidia slender, slightly curved, multiseptate, $40\text{--}75 \times 3\text{--}3.5\ \mu$, hyaline.

On tobacco it causes leaf spots. The sporiferous hyphae are abundant near the center of the disease spots.

C. apii Fr.

Spots amphigenous, subcircular, pale-brown, 4–6 mm. in diame-

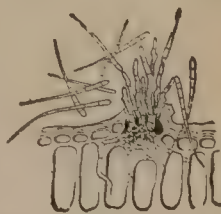


FIG. 386.—*C. nicotianæ*. After Sturgis.

ter, with a more or less definite elevated margin; conidiophores hypophyllous, light-brown, fasciculate, continuous or 1 or 2-septate, subundulate, $40-60 \times 4-5 \mu$; conidia hyaline, obclavate or almost cylindric, 3 to 10-septate, slender, $50-80 \times 4 \mu$.

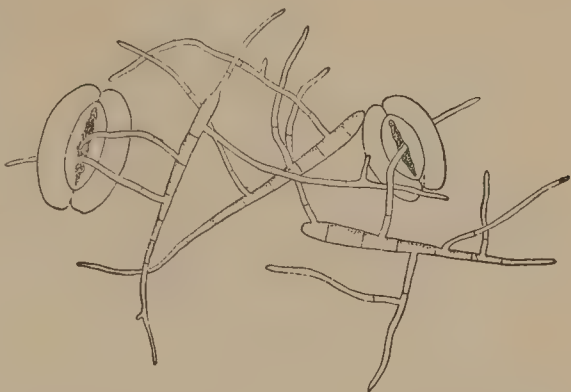


FIG. 387.—*C. nicotianæ*, spores germinating and entering stomata. After Sturgis.

A serious leaf spot is produced on celery, parsnips, etc.

***C. beticola* Sacc.**

Spots amphigenous, brownish, purple-bordered, becoming ashy centered; conidiophores fasciculate, short, simple, erect, flavous, $35-55 \times 4-5 \mu$; conidia elongate, filiform obclavate, hyaline, multiseptate, $75-200 \times 3.5-4 \mu$.

This fungus causes a very serious disease of beet, producing spots on the leaves. Found also on spinach. The conidiophores usually, though not always, emerge from the stomata from a few-celled stroma and are amphigenous. They vary in length and septation with age. If in humid atmosphere the spots become hoary, due to the large number of spores present. Each cell of the spore is capable of germination. The germ tubes infest the host through the stomata. Pure cultures of the fungus may readily be secured by the usual methods. Here the mycelium produces dense matted colonies of deep olive color and a greenish-gray aerial growth but no conidia.



FIG. 388.—*C. apii*. After Duggar and Bailey.

C. fusca Rand.=*Calsterosporium diffusum* Heald and Wolf.

Leaf spots up to 10 or 15 mm. in diameter, at first somewhat angular and bounded by the veins, becoming roundish to irregular, dark reddish brown on both leaf surfaces; mycelium dark brown and septate, intercellular, sometimes also creeping over the leaf surfaces; conidiophores mostly epiphyllous, short and erect, typically in dense, tawny clusters from stromata, developed beneath the epidermis and later bursting through, also arising singly from the prostrate surface mycelium; conidia pale olive brown, highly variable in size, 30–100 μ or more by 3–6 μ , usually curved, typically subclavate, multicellular.

On pecan leaves.

C. cucurbitæ E. & E.

Spots amphigenous, rounded, subochraceous, becoming thin and white, 1 to 4 mm. in diameter, border slightly raised; conidiophores tufted, olive-brown, 70–80 x 4 μ , continuous, subgeniculate above, apically obtuse; conidia linear clavate, 100–120 x 3–4 μ , hyaline, septate.

On cucumbers, associated with *Phyllosticta cucurbitacearum*.

Others are on apple, fig, grape, *Rubus*, *Citrus*, coffee, spinach, egg-plant, watermelon, okra, pepper, horseradish, peanut, castor bean, cowpea, bean, clover, asparagus, water lily, violet, hollyhock, rose, phlox, oleander, *Tecoma*, orchids, geranium, mignonette, *Odon-toglossum*, lily, calla, mulberry, ash, butternut, catalpa, linden, maple, pecan, redbud, sequoia, willow.



FIG. 389.—Fertile hyphæ and spores of *C. beticola*. After Duggar.

Stilbaceæ (p. 377)

Sterile hyphæ creeping, scanty; fertile hyphæ collected into a stalk-like or stroma-like fascicle, bearing conidia at the top, more rarely along the sides, pale, bright-colored or dark.

Hyalostibeæ-Amerosporæ

Bright or light-colored, conidia globose, elliptic or oblong, continuous.

KEY TO GENERA OF *Hyalostibææ-Amerosporæ*

Conidial part distinctly capitate or at least terminal

Conidia not in chains; head of conidia not gaping or splitting above, not spiny; conidiophores of head normal; conidia covered with mucus; synema moncephalous; conidiophores not dendroid-verticillate.....

1. *Stilbella*, p. 417.

Conidia in chains; synema with conidia above, not pubescent; conidia without mucus.....

2. *Coremium*, p. 417.

Stilbella Lindau

Hyphæ forming a coremium which is capitate above; conidiophores borne on the cap; conidia small, often enclosed in slime.

Over one hundred species chiefly saprophytes. (Commonly known as *Stilbum*, but the type of that genus being a hymenomycete it was renamed.)

S. populi on poplar=*Mycosphærella populi*. Other species do serious injury to coffee and tea.

Coremium Link

Coremium cylindric, apically enlarged and fertile; conidia very small, catenulate. A small genus. In part=*Rosellinia* and *Penicillium*. See p. 163 and p. 125.

Phæostilbææ-Phragmo-
sporæ

Conidia 3 to several-celled, oblong to cylindric, dark or hyaline.

Isariopsis Fries

Slender, dark or subhyaline, cylindric hyphæ laxly aggregated; conidia in a lax panicle or head, cylindric or clavate. See Fig. 391.



FIG. 390.—*Coremium glaucum*.
After Corda.



FIG. 391.—*Isariopsis*.
After Saccardo.

I. griseola Sacc.

Spots hypophyllous, ochraceous; coremium stipitate, dense. 200 x 30–40 μ , composed of filiform hyphæ; conidia borne on the reflexed ends of the hyphæ, cylindric-fusoid, curved, 50–60 x 7–8 μ , gray, 1 to 3-septate, constricted.

It causes disease of beans.

Tuberculariaceæ (p. 377)

Hyphæ compacted into a globose, discoid or verruciform body, the sporodochium; sporodochia typically sessile, waxy or subgelatinous, white, bright-colored or dark to black.

In part=Nectria, Claviceps and Hymenoscypha, etc. See pp. 109, 148, 151.

Tuberculariaceæ-Mucedineæ-Amerosporæ

Conidia hyaline or bright-colored, continuous, globose to fusoid; hyphæ hyaline.

KEY TO GENERA OF Tuberculariaceæ-Mucedineæ-Amerosporæ

Sporodochia smooth or nearly so; conidia muticate

Conidia not covered with mucus

Conidia not acrogenous-capitate; sporodochium without a heterogeneous cup; conidia not catenulate or scarcely so, arising on outside of hyphæ; conidiophores present

Conidia pleurogenous or acropleurogenous, ovoid to oblong....

1. **Tubercularia**, p. 419.

Conidia acrogenous; conidiophores not verrucose, not uredinicolous; sporodochia verruciform or effuse; conidiophores simple, not united or radiate.....

2. **Sphacelia**, p. 420.

Conidia covered with mucus; sporodochia verruciform or subeffuse.....

3. **Illosporium**, p. 420.

Sporodochia ciliate at the margin; sporophores distinct; conidia not in chains; conidiophores not ciliate or united....

4. **Volutella**, p. 420.

Tubercularia Tode (p. 418)

Sporodochium tubercular or wartlike, sessile or subsessile, smooth, rarely with bristles, usually reddish; conidiophores very slender, usually branched; conidia apical, ovate to elongate. In part = *Nectria*. See p. 148.

Over one hundred species, chiefly saprophytes.

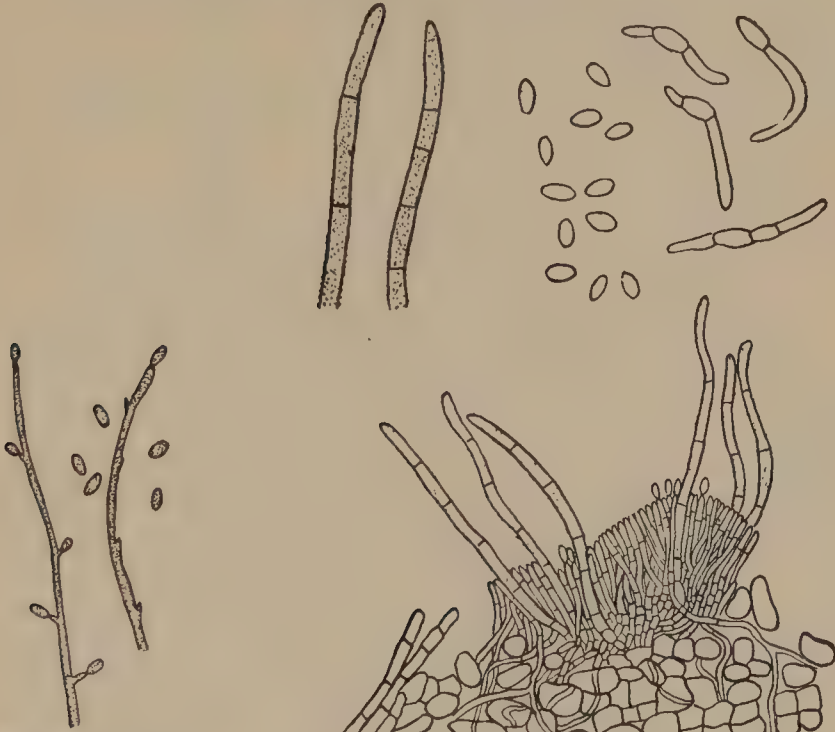


FIG. 392.—Hyphæ of *Tubercularia*, bearing conidia. After Durand.

FIG. 393.—*T. fici*, sporodochium, showing setæ and conidial formation. After Edgerton.

T. vulgaris Tode = *Nectria cinnabarina*. See p. 148.

T. fici Edg.

Sporodochia scattered or gregarious, superficial or subcuticular, light pink, variable in size up to 3–4 x 1–1.5 mm., smooth, irregular in outline; conidiophores crowded, hyaline, 20–27 x 1–2 μ ; conidia small, clear, elliptic to oval, regular in size, 5–7 x 2.5–5 μ ; setæ scattered or abundant, variously placed, straight or curved, hyaline or subhyaline, septate, papillose, 60–90 x 4–6 μ .

It is the cause of a fig canker.

Sphacelia Léviellé (p. 418)

Sporodochia planose, effuse, stromate or sclerotioid; conidiophores short, simple, filiform; conidia apical, ovate.

A small genus, chiefly conidia of *Claviceps* and related genera.

S. segetum Lév. = *Claviceps purpurea*. See p. 151.

Illosporium Martius (p. 418)

Sporodochia wartlike, pulvinate or subeffuse, white or light-colored, subgelatinous or waxy; conidiophores variable; conidia globose, sigmoid, variable, embedded in mucous. There are some forty species.

I. malifoliorum Shel.

Spots suborbicular or coalescing and becoming irregular, brown or mottled with gray and with a small gray spot near the center, 5–15 mm. in diameter; sporodochia hypophyllous, minute, gelatinous, yellow-amber, becoming black, spherical, becoming discoid or irregular, 150–160 μ in diameter; conidiophores branched; conidia oblong, 1–3.5 x 4 μ .



FIG. 394.—*Illosporium maculicola*.
After Saccardo.

It is said to be one of the common and destructive causes of leaf spots of the apple often resulting in nearly complete defoliation. In the centers of the leaf spots other spots bearing other species of fungi are often found, leading to the thought that perhaps the *Illosporium* in such cases results from secondary infection in the wounds made by the earlier fungus. The sporodochia are hypophyllous, often hidden by the normal pubescence of the leaf.

Volutella Tode (p. 418)

Sporodochia discoid, regular, margin ciliate, sessile or stipitate; conidiophores usually simple; conidia ovoid to oblong.

Some seventy species.

V. leucotricha Atk.

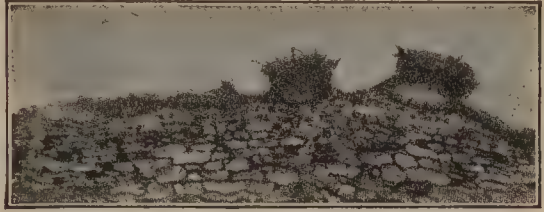
Sporodochia convex-discoid, white to pale flesh-color; setæ few, filiform, few-septate, subhyaline; conidiophores densely fasciculate, filiform; conidia oblong.

On cuttings in greenhouses.

V. fructus S. & H.

Spots on the fruit, circular; sporodochia, numerous in concentric

circles, cubecuticular, erumpent, elevated 200–250 μ , 150–400 μ in diameter; mycelium black; setæ distributed throughout the sporodochium, black, 0 to 3-septate, acute, smooth, 100–400 x 5–8 μ ; conidiophores elongate, hyaline, simple, 25–35 x 3 μ ; conidia smooth, oblong-fusoid to falcate-fusoid, hyaline or sub-olivaceous, 17–23 x 2.5–3.5 μ .



It is the cause of a dry rot of apples.

FIG. 395.—*V. fructus*. Sporodochia in section. After Stevens and Hall.

V. lycopersici Pritchard and Porte¹ causes collar-rot of tomatoes, killing young plants by girdling the stem.

Other species are on carnation and *Bletia*.

Tuberculariaceæ-Mucedineæ-Phragmosporæ

Hyphæ hyaline; conidia 2 to several-septate, hyaline or bright-colored, fusoid to falcate, rarely short and simple.

Fusarium Link²

Conidia often of diverse types; the larger ones (macroconidia) wedge shaped, fusiform, falcate, or uncinuate, more or less pointed toward or at apex; smaller conidia, microconidia, either of similar shape, though smaller in size and continuous, or with fewer septa, or of a distinct type, oblong, ovate, reniform, lanceolate, etc.; conidiophores simple to compoundly subverticillate, produced on loose mycelium or over a flat or tuberculate layer of pseudoparenchyma; conidia terminal, single or in small or large balls, in buttery layers, pseudopionnotes, in gelatinous layers, pionnotes, or in separate tubercular masses, sporodochia; microconidia in some cases catenulate; neither conidia nor mycelium ever gray or black but from hyaline to various hues of blue, yellow, brown, purple, and red.

Due to the fact that many of the *Fusaria* produce spores in sporodochia, wart-like bodies composed of conidiophores and masses of conidia, the genus is usually placed under the Tubercu-

¹ Pritchard, F. J. and Porte, W. S. Collar-rot on Tomato. Jour. Agr. Res. 21: 179, 1921.

² The manuscript regarding this genus was prepared by C. D. Sherbakoff.

lariaceæ. The forms that produce conidia over a gelatinous layer of mycelial growth were formerly placed in the same family but in the genus *Pionnotes*; the forms with very short conidiophores were referred to the genus *Fusoma* in the *Moniliaceæ*. Some have also been placed in the genera: *Cephalosporium*, *Trichothecium*, *Arthrosporium*, *Sporotrichum*, *Spicaria*.

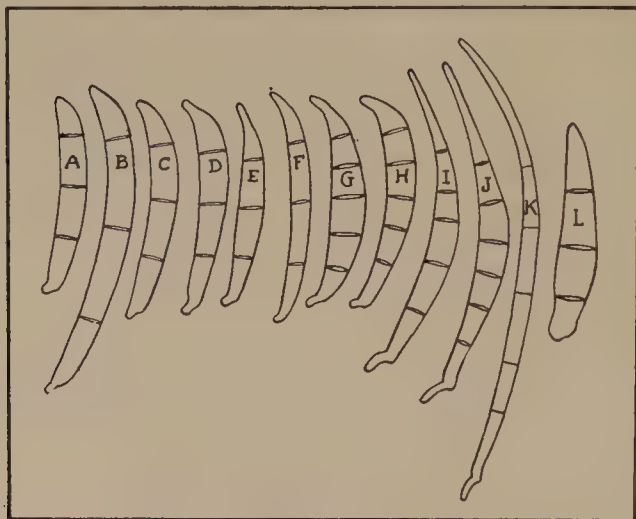


FIG. 396.—A-C, Section Martiella: A, *F. solani*; B, *F. martii*; C, *F. cœruleum*; D-E-F, Section Elegans: D, *F. redolens*; E, *F. oxysporum*; F, *F. orthoceras*; G-H, Section Discolor: G, *F. culmorum*; H, *F. sulphureum*; I-J, Section Gibbosum: I, *F. falcatum*; J, *F. scirpi*; K, Section Roseum: *F. avenaceum*; L, Section Ventricosum: *F. agrillaceum*. All conidia drawn from pure cultures on steamed plant stems. Redrawn after Wollenweber.

The ascigerous connection is in part with *Nectria*, *Neonectria*, *Neocosmospora*, *Gibberella*, *Calonectria*, *Hypomyces*, and *Sphærostilbe*.

This is a large genus in which many species have been described. However, many of the descriptions are entirely inadequate, therefore, many of the names are relegated to synonymy. Some of the species are destructive parasites, invading the ducts of plants and by stoppage of the water supply (Fig. 398), causing the class of disease known as "wilts." Others induce rot, spotting, cankers, etc. Taken as a whole the genus is one of the most injurious with which plant pathology has to do.

It seems probable that some of the forms that live normally as saprophytes in soil may encroach upon living roots of susceptible plants when these are available. Biologic specialization has been found, in that forms apparently morphologically indistinguishable

are frequently incapable of cross inoculation onto other than their usual hosts.

Most *Fusaria* grow well in culture, and the species often show marked differences in growth on various media, particularly in the colors that are developed, however, some of the species deteriorate very rapidly when carried on common artificial media.

As with the anthracnoses much study is here needed to throw light on the inter-relation of the various species and their hosts. Appel and Wollenweber¹ and later others have made extensive studies of many species to lay the ground for a monograph. At present it is accepted that in delineating species strictly standard culture conditions should be used and that the important char-

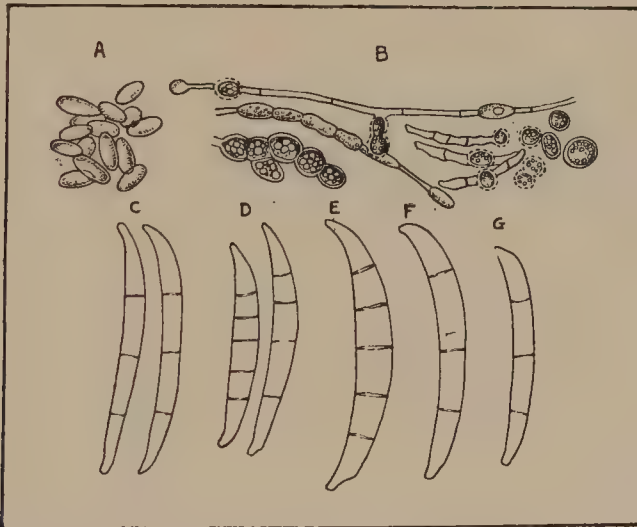


FIG. 397.—A, *F. batatatis*, microconidia; B, *F. batatatis*, chlamydospores; C, *F. batatatis*, conidia; D, *F. hyperoxysporum*; E, *F. culmorum*; F, *F. radiculicola*; G, *F. orthoceras* var. *triseptatum*. Redrawn after Wollenweber.

acters are: the mode of production of conidia and their form, especially shape of their bases, apices, degree and type of curvature (see Fig. 399) and septation; the color of the mycelium and spores; and the presence, or absence, and type of chlamydospores, sclerotia, and microconidia.

The two following genera closely resemble *Fusarium* and are often mistaken for it:

¹Appel, O & Wollenweber, H. W. Grundlagen einer Monographie der Gattung *Fusarium* (Link). Arb. Kais. Biol. Anstalt f. Land u. Forst 8:1, 1910. Wollenweber, H. W. Studies on the *Fusarium* problem. Phytrop. 3: 24, 1913.

I. *Ramularia* (Unger) Fries. It differs from *Fusarium* primarily in that the conidia typically are not curved, nearly cylindric, with a more or less rounded apex and not pedicellate.

Fusarium candidum Ehr. = *Ramularia candida* (Ehr.) Woll.

II. *Cylindrocarpon* Woll. differs from *Fusarium* in that the conidia are typically cylindric to subcylindric, with both ends rounded.

Fusarium album Sacc. = *Cylindrocarpon album* (Sacc.) Woll.

The following are a few of the *Fusaria* and *Fusaria*-like fungi

which at present are considered to be conidial forms of certain ascomycetes:¹

Fusarium fructigenum Fr.
v. *majus* Woll. = *Gibberella juniperi* (Desm.) Woll.

Fusarium graminearum Schwabe = *Gibberella saubinetii* (Mont.) Sacc.

Fusarium mali All. (= *Cylindrocarpon*) = *Nectria galligena* Bres.

Fusarium minimum Fel. = *Calonectria graminicola* (Berk. & Br.) Woll.

Fusarium pallens (Nees.) Link = *Sphaerostilbe coccophila* Tul.

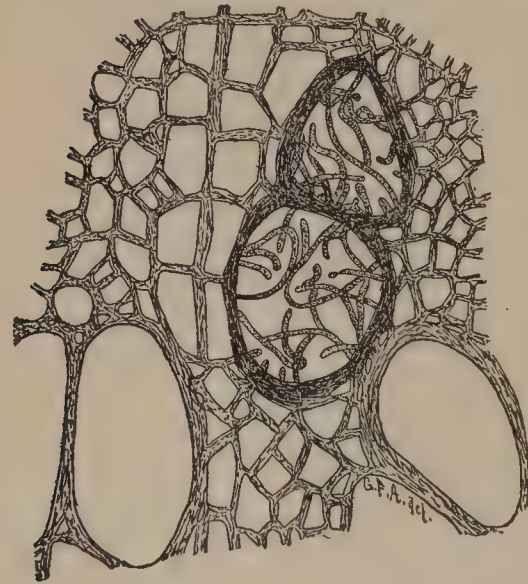


FIG. 398.—*F. vasinfectum*, showing thrombosis of veins. After Atkinson.

Fusarium pyrochroum (Desm.) Sacc. = *Gibberella euonymi* (Fel.) Sacc.

Fusarium salicis Fel. = *Gibberella effusa* Rehm.

Fusarium sphæriæ Fel. = *Hypomyces leptosphæriæ* (Niessl) Woll.

Fusarium urticarum (Cda.) Sacc. = *Gibberella moricola* (Ces. & de Not.) Sacc.

Fusarium willkommii Lind. (= *Cylindrocarpon*) = *Nectria ditissima* Tul.

Cylindrocarpon ianthothele Woll. = *Hypomyces rubi* (Osterw.) Woll.

Ramularia magnusiana (Sacc.) Lind. = *Neonectria ramulariæ* Woll.

¹ Wollenweber, H. W. *Fusaria autographice delineata*, Ann. Myc. 15:34, 1917.

KEY TO SECTIONS OF *Fusarium* ¹

- Conidia in perennial, true pionnotes; aërial mycelium typically absent, slow growing fungi Section **Eupionnotes**.
- Conidia in pseudopionnotes, or in sporodochia, or in small balls, sometimes in chains, or single; aërial mycelium in cultures usually present
- Chlamydospores intercalary to none
- Quasi *Fusaria*, i. e., possessing microconidia of conspicuously different types than those of true *Fusaria*
- Microconidia pyriform Section **Sporotrichiella**.
- Microconidia lanceolate, 0 to 3-septate Section **Arthrosporiella**.
- Microconidia in chains
- Macroconidia thick-walled, mostly 6 and more septate Section **Specarioides**.
- Macroconidia thin-walled, mostly 3 to 5-septate Section **Moniliforme**.
- True *Fusaria*; sporodochia convex, macroconidia pedicellate, microconidia rare; sometimes blue sclerotia present
- Conidia typically narrow, not noticeably broader in diameter near the middle
- Conidia gradually attenuated Section **Roseum**, p. 431.
- Conidia pinched near apex
- Conidia with thin walls Section **Laterium**.
- Conidia with more or less thick walls
- Conidia uniform, chlamydospores common Section **Discolor**, p. 430.
- Conidia more or less variable, no chlamydospores Section **Saubinetii**.
- Conidia mostly noticeably wider in diameter near the middle; not pinched near apex.
- Chlamydospores present Section **Gibbosum**, p. 431.

¹ The first key to sections covering a considerable number of the species was given by C. D. Sherbakoff, *Fusaria* of Potatoes, Cornell Univ. Agr. Exp. Sta. Mem. No. 6, 1915. Another key covering a wider range of the species was published by Wollenweber, "Conspectus analyticus *Fusarium*," *Berichten d. deut. Bot. Ges. Jahrg.* 1917, 35, H. 10: 732-739.

- Chlamydospores terminal and intercalary; frequently plectenchymic substrata and also dark colored sclerotia occur
- Conidial walls and septa thin; macroconidia pointed toward apex... Section **Elegans**, p. 427.
- Conidia thick-walled, with thick septa
- Conidia at apex obtuse to obliquely subrounded, no ascigerous stage known..... Section **Martiella**, p. 429.
- Conidia at apex sometimes pointed, conidial stage of Hypomyces Section **Pseudomartiella**.
- Chlamydospores terminal; no pionnotes, no tubercular sporodochia; growth floccous; conidia subcurvate, apex slightly attenuate, apedicellate..... Section **Ventricosum**, p. 432.

Section **Moniliforme**

Microconidia continuous, oval to short spindle-shaped, single or in chains, balls, pseudopionnotes, and sporodochia; macroconidia single or in pseudopionnotes and sporodochia, in some species rare, in others abundant, usually slightly curved toward apex, with very thin walls and septa, slightly pinched at apex, usually pedicellate; mostly 3-septate and measure $25-40 \times 2.5-4.5 \mu$; some 4 and 5-septate; aërial mycelium mostly hyaline to grayish or bluish purple, well-developed to very scant; substratum on glucose agars colorless to dark grayish or bluish purple; no chlamydospores; in certain species production of minute, blue sclerotia like bodies, probably immature perithecia of a *Gibberella*, are common on certain media, steamed sweet potato plugs, etc. *Fusaria* of this section superficially much resemble those of section *Elegans*; however, they are of a distinct group in having no true chlamydospores, in microconidia borne in chains and of a short spindle-shape; in the shape of macroconidia; and in undoubted connection with some *Gibberella* species, probably *G. acervalis* (Moug.) Woll.

A species of this section, **F. moniliforme** Sheldon, was recorded as causing mold of corn ears, first in Nebraska and now in practically every other state. The same species, or one closely related to it, was found to cause damping off of coniferous seedlings in the United States.

Section **Elegans**

All species have microconidia, mostly unicellular, scattered or in balls, ellipsoidal or reniform, averaging $5-12 \times 2-3.5 \mu$; sickle-shaped conidia, macroconidia, (Fig. 396, D, E, F) mostly 3-septate, usually $25-40 \times 3-4.5 \mu$, but also 4 and 5-septate, usually $40-50 \times 3-4.5 \mu$. Sporodochia, with or without a sclerotial base, are common; pseudopionnotes also often present. Conidia in masses mostly salmon-colored, sometimes brownish white or brilliant orange. Conidiophores single to compoundly subverticillate. Chlamydospores ellipsoidal to round, terminal and intercalary, mostly unicellular and measuring $5-10 \mu$. Ascigerous stage unknown.

Many of the forms in this group are vascular parasites though sometimes causing parenchyma rot. Distinctive characters of better known species of economic importance are given in the following annotated key.

KEY TO SPECIES OF SECTION **Elegans**

No sporodochia, pseudopionnotes, or sclerotia; macroconidia few. Subsection **Orthocera**.

Mycelium yellowish **F. citrinum** Woll. On decaying tomato fruit

Mycelium not yellowish

Rice cultures wine-red. **F. orthoceras** App. & Woll. In Irish potato roots and tubers and in tomato stems, Fig. 397 G

Rice cultures not wine-red. **F. conglutinans** Woll. Vascular parasite of cabbage and aster

Sporodochia typically present. Subsection **Oxysporum**.

Sclerotia blue. Series **Cyanostroma**.

Macroconidia considerably curved. **F. tracheiphilum**, E. F. Sm.

3-septate conidia $25-35 \times 3.25-4 \mu$; 4 and 5-septate rare. Vascular parasite of cowpeas.

Macroconidia moderately curved

Macroconidia comparatively narrow, nearly cylindric through greater part of their length; **F. batatatis** Woll. (Figs. 397, A-C); occasionally found to cause wilt (stem rot) of sweet potatoes; **F. bulbigenum** Cke. & Mass., morphologically appears to be the same as the preceding species; of the same type and size of macroconidia, 3-septate, $25-50 \times 2.75-3.75 \mu$; 4 and 5-septate, $30-50 \times 3-4 \mu$; on rotted bulbs of narcissus, decaying tubers of Irish potatoes and on apples

Macroconidia comparatively broad and wider about the middle

Macroconidia in numerous, small sporodochia

3-septate conidia 35×4.3 ($30-40 \times 4.0-4.6$) μ ; 4 and 5-septate common, averaging 40×4.4 μ ; blue sclerotia large (on steamed potato tuber plugs); **F. sclerotioides** Sherb. In vascular systems of Irish potato and corn stems.

3-septate conidia 30×4.3 ($25-35 \times 3.5-4.5$) μ ; 4 and 5-septate conidia rare; blue sclerotia small; **F. blasticola** Rostrup.

In vascular system of potato tubers and on pine seedlings.

Macroconidia in few, large sporodochia; pionnotes (pseudo) not conspicuous, not continuous.

3-septate conidia up to 100%, 30×4 ($25-40 \times 3.25-4.5$) μ ; 4 and 5-septate very rare to none; **F. oxysporum** Schlecht.

Vascular parasite causing wilt of Irish potatoes, also found on tomatoes, cowpeas, peas and sweet potatoes.

F. mali Taub., the cause of onion pink root, is not closely related to **F. oxysporum**, but much resembles **F. solani**.

3-septate conidia $30-50 \times 3-4.25$ μ ; 4 and 5-septate common; **F. niveum** E. F. Sm. Vascular parasite causing wilt of watermelons.

3-septate conidia about 60-80%, 35×4.25 ($30-40 \times 3.5-4.5$) μ ; 4 and 5-septate 20 to 40%, 5-septate 43×4.25 ($40-45 \times 4-4.5$) μ ; **F. auranticum** (Link) Sacc. In living stems of Irish potatoes, decaying cucurbits, corn, Lagenaria and Rubus.

Macroconidia inconspicuous, continuous pionnotes (pseudo)

Macroconidia somewhat narrow, mostly 3-septate, $27-28 \times 3-3.75$ μ ; 4 and 5-septate few; **F. vasinfectum** Atk. Vascular parasite producing wilt of cotton and okra.

Macroconidia somewhat broad, 4 and 5-septate common; 3-septate 34×4.1 ($25-45 \times 3.5-4.25$) μ ; **F. hyperoxysporum** Woll. (Fig. 397, D) (= **F. lutulatum** Sherb.). Causes stem rot of sweet potatoes; also rot of Irish potato tubers.

Sclerotia pale to none. Series **Pallens**.

Conidia slightly broader near the middle septum; not pinched at apex

Sporodochia poorly developed; mycelium tremelloid-effuse, readily decumbent, plectenchymatic sclerotia ochrous. **F. euoxysporum** Woll. 3-septate conidia 35×3.5 ($30-42 \times 3-4.5$) μ ; 4 and 5-septate rare. Found in vascular system of potato tubers, and also causing potato tuber rot.

Sporodochia numerous, often confluent

Growth on agars in plate distinctly zonate. 3-septate conidia averaging 33×4.2 μ ; 4 and 5-septate conidia few, 5-septate $39-4.6$ μ . **F. zonatum** (Sherb.) Woll. On rotted potato tubers

Growth on agar in plates not zonate, macroconidia often in pionnotes (pseudo); 3-septate conidia up to 100%, 30–40 x 3.3–3.5 μ . **F. lycopersici** Sacc. Vascular parasite causing wilt of tomatoes

Conidia broader at the upper third septum, somewhat pinched near apex

Pionnotes present. 3-septate conidia 36 x 4.8 (31–41 x 4.3–5) μ ; 4 and 5-septate not many. Chlamydo-spores when 0-septate about 8.5 x 9 μ . **F. redolens** Woll. Causes stem rot of *Pisum sativum* (Germany), found also on rotted potato tubers (New York).

No pionnotes; sporodochia sometimes numerous, medium to large; 3-septate conidia 35 x 5.25 (27–43 x 4.8–6.3) μ ; 4-septate rare, no 5-septate; chlamydo-spores, when 0-septate, 11 (6–18) μ . **F. spinaciae** Sherb. Causes root rot of spinach.

Section Martiella

The species have conidia of the form shown in Fig. 396, A, B, C. Chlamydo-spores present. No ascus stages known.

Fusarium cœruleum (Lib.) Sacc. (Fig. 396, C).

Conidia normally triseptate, averaging 30–40 x 4.5–5.5 μ , seldom 4 and 5-septate. Conidial mass brownish white and yellow ochre to reddish ochre. Plectenchymatic stroma chiefly violet to indigo-blue and bluish black; by infiltration with the latter color the conidial mass may become bluish green as in other species of the section Martiella. *F. cœruleum* is the only species of this section having reddish ochre conidial masses. Chlamydo-spores as in other species of the section. Cause of potato tuber rot.

F. martii App. & Woll. (Fig. 396, B). Conidia mostly non-septate, single, or in pseudopionnotes and sporodochia and then mostly 3 and 4-septate; 3-septate 44 x 5.15, 30–51 x 4.9–5.3 μ , 4-septate 49 x 5.3 (48–50 x 4.9–5.4) μ , 5-septate from rare to 7 per cent; color of conidial mass deep lichen to green and dark blue. Saprophyte, at least does not cause potato tuber rot, bean dry rot, or stem rot of garden peas.

F. martii phaseoli Burkh. morphologically is about the same as *F. martii* but differs from it by causing dry root rot of several different beans of the genus *Phaseolus*, of black-eye cowpea (*Vigna sinensis*) and of kulti bean (*Dolichos biflorus*).

F. solani (Mart. p. par.) App. & Woll. (Fig. 396 A). Microconidia always present, at least on aërial mycelium; macroconidia often slightly broader in their upper half, typically 3-septate, 30 x 5.5, 25–35 x 5.4–5.8 μ , 4-septate from few to 5 per cent, 5-septate

from none to 0.5 per cent. Very common saprophyte on potato tubers and other substrata; cause of a gray rot of economic aroids.

F. eumartii Carp. Macroconidia in their protoplasmic appearance often are strikingly similar to *F. cœruleum*; mostly 4 to 6-septate, $54-75 \times 5.5-6.6 \mu$; conidial masses in exposed pseudopionnotes brownish white to bright brown and, through absorption of the color from substratum, becoming gray and blue-gray; aërial mycelium weakly developed; chlamydospores $7-10 \mu$. It causes potato tuber and stem rot.

F. radicicola Woll. Conidia normally 3-septate (Fig. 397, F), less often 4 or 5-septate, scattered or in sporodochia or pionnotes

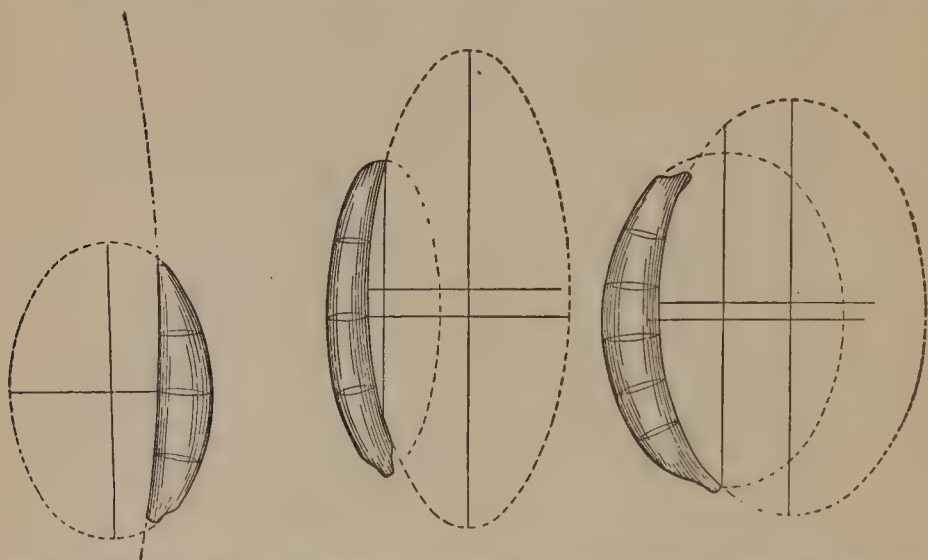


FIG. 399.—Spores of *Fusarium* showing curvature in different species. *F. sp.*, *F. cœruleum*, *F. culmorum*. After Appel and Wollenweber.

averaging $30-45 \times 3.75-4.5 \mu$. Chlamydospores $7-10 \mu$. On partly decayed tubers and roots of plants, particularly on white potato and sweet potato. Cause of the jelly end rot and lenticel dry rot of potato tuber and rot of potato stem.

Section *Discolor*

Conidia of the form type shown in Figure 396 G, H. Intercalated chlamydospores present. Ascigerous stage unknown.

F. culmorum (W. G. Sm.) Sacc. (Figs. 396, G, 397, E).=*F. rubiginosum* App. & Woll.

This differs from the conidial stage of *Gibberella saubinetii*

sharply in type of conidia and in the presence of clusters and chains of intercalated chlamydospores and it has no connection with the ascus stage.

Conidia scattered in sporodochia or in pionnotes, in masses ochraceous to salmon colored, 5-septate, averaging $30-45 \times 5.5-7 \mu$, seldom 3 to 4-septate, rarely with a larger or smaller number of septa. The slight constriction at the apical end and the pedicellate base of normal conidia makes this fungus a type species of the section *Discolor*. Chlamydospores intercalated, single, in chains or in clusters, averaging $7-14 \mu$ in diameter.

Common on partly decayed plants. It is a wound parasite on cereals and causes root rot. It has been found on the following hosts: *Zea*, *Triticum*, *Hordeum*, *Solanum*, *Cucurbita*.

F. trichothecioides Woll. In contrast to the other species of the section *Discolor* this forms two sorts of conidia: (1) The comma type, formed as a slightly curved comma rounded at both ends; and (2) the normal macroconidia, typical of the section. It is a wound parasite, the cause of dry rot of potato tubers.

Section *Gibbosum*

Conidia of the form shown in Figure 396, I, J. Intercalated chlamydospores. Ascigerous stage unknown.

F. falcatum App. & Woll. (Fig. 396, I)

Conidia 5-septate, $35-55 \times 4-5 \mu$, parabolically curved. A wound parasite, cause of tomato fruit rot.

F. scirpi Lamb. & Fautr. (Fig. 396, J.) (= *F. gibbosum* App. & Woll.)

Conidia 5 (5-7) septate, $30-60 \times 4-5.2 \mu$, hyperbolically curved. Probably a cause of potato tuber rot.

F. sclerotium Woll.

This differs from *F. scirpi* in having spherical, blue sclerotia. Conidia mostly 5-septate. A wound parasite, the cause of fruit rot on tomato and watermelon.

Section *Roseum*

Conidia of the form-type shown in Figure 396 K. No true chlamydospores but as a rule sclerotia, blue in a number of species. Ascigerous stage unknown.

F. avenaceum (Fr.) Sacc. (= *F. subulatum* App. & Woll.) Fig. 396, K, N.

Saprophytic on various dead substances; a wound parasite

only under conditions of high humidity and closed air; sometimes causes scab and seedling blight of cereals and dry rot of potato tubers.

Section *Ventricosum*

Conidia of the form-type shown in Figure 396, L. No sporodochia. Chlamydospores terminal only. Ascigerous stage unknown.

F. agrillaceum (Fr.) Sacc. (Fig. 396, L).=*F. ventricosum* App. & Woll.

Conidia never formed in sporodochia, brownish-white to cream colored, 3-septate, $29-37 \times 5.75-7.5 \mu$. Conidiophores bostryx-like or irregularly branched. Chlamydospores terminal only. Wound parasite, cause of a tuber rot of potato.

Several species that have not yet been critically studied nor assigned to places in the sections given above are said to be the cause of a disease. They are given below.

F. rubi Wint.=*Ramularia rubi* (Wint.) Woll.

Mycelium white, becoming pink, especially abundant on the flowers; conidia elongate, 1 to 8-septate, variable in size and form, straight or curved, $14-30 \times 3-3.5 \mu$, not constricted.

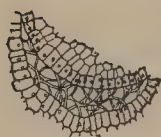


FIG. 400.—*F. rubi*, section of ovary showing mycelium between carpel and ovule. After Cook.

Cook found this fungus in diseased buds of dewberries and by inoculation demonstrated that it is responsible for witches' broom, double-blossom, and similar abnormal growths of this plant.

F. rhizogenum P. & C.

Sporodochia superficial, 1 to 2 mm. wide, dense, convex, white or whitish, hyphæ densely interwoven, septate, subramose; conidia oblong, roundish, 1-septate, $70 \times 4 \mu$.

It was originally described as a parasite on apple roots in Nebraska. The mycelium grows within the roots and gummosis of the wood occurs. Microconidia are known, also chlamydospores.

F. cubense E. F. Sm. was isolated from bananas affected with blight. Inoculation showed the fungus capable of growing through the bundles for long distances.

F. limonis Bri.

Sporodochia gregarious, confluent, white; hyphæ spreading, branched, septate; conidiophores erect, with alternate or opposite branches; conidia variable, acrogenous, continuous to 3-septate,

oblong to fusiform, curved, pointed, slightly constricted, $26-27 \times 2.4-2.8 \mu$.

This fungus is held to be contributory to, if not responsible for, the Mal-di-gomma or foot rot of citrous fruits which is known practically wherever these fruits are cultivated.

F. lini Boll.

Sporodochia erumpent, compact, cream to flesh-colored; conidiophores short, much branched; conidia 3-septate, fusiform, slightly curved to falcate, $27-38 \times 3-3.5 \mu$.

A serious, widespread flax wilt is caused. The mycelium develops luxuriantly from bits of diseased stem laid in sterile Petri dishes and grows well in culture media. Normally a soil saprophyte, it invades the roots, grows through the veins, plugs the ducts and causes death. The sporodochia are found abundantly on the bases of diseased plants.



FIG. 401.—*F. lini*. After Bolley.

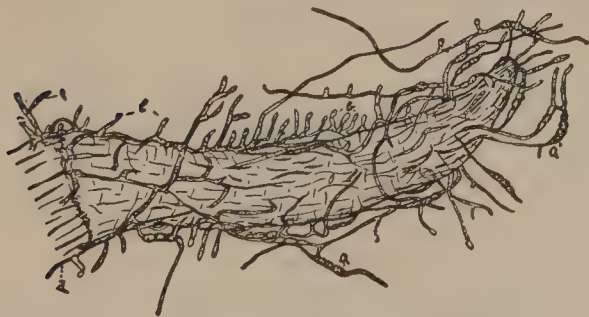


FIG. 402.—*F. lini*, sketch, showing the mode of attack upon a young root tip of a seedling flax plant. After Bolley.

The spores abound on all diseased parts particularly on the seeds. Infection experiments have demonstrated its pathogenicity.

F. violæ Wolf

Infected areas dark, sunken; sporodochia within the host; conidia fusiform-falcate,

$28-38 \times 4-6 \mu$, 3 to 5-times septate; hyphæ hyaline, $4-7 \mu$ in diameter, irregularly branched. It causes a disease of roots and stems of pansy.

Others are on fig, celery, pea, tobacco, corn, alfalfa, carnation, chrysanthemum, Colocasia, sweet pea, onion, ricinus, cacao, Pelargonium, cabbage, rice, etc.

Tuberculariaceæ-Dematieæ-Phragmosporæ

Hyphæ dark; conidia usually colored, 2 to several-septate, oblong to cylindric.

KEY TO GENERA OF Tuberculariaceæ-Dematieæ-Phragmosporæ

- Conidia in chains; sporodochium discoid. 1. **Trimmotostroma**, p. 434.
 Conidia not in chains, muticate; sporodochium smooth; conidia not proliferate and united; sporodochia convex-pulvinate. 2. **Exosporium**, p. 434.

Trimmotostroma Corda

Sporodochia pulvinate, compact, bearing a layer of conidiophores; conidia oblong, often curved, 2 to 8-septate, catenulate, brown.

A genus of a half dozen species.

T. abietina Doh.

Mycelium perennial; sporodochia foliicolous or cauliculus, diffuse; conidiophores subhyaline or tinged with olive-brown, $4.5 \times 20-30 \mu$, septate, sparsely branched, bearing the conidia terminally; conidia catenulate, very variable, dark olivaceous-brown, slightly roughened, usually oblong, spherical, straight or inequilateral, continuous, 5μ , or 2 to 5-celled and $5-6 \times 8-16 \mu$, not constricted, rarely muriform, $5 \times 10 \mu$.

On white and balsam firs. The perennial habit of the mycelium makes the pest a persistent one and as no conidia are produced till the second year after infection its presence is the more readily overlooked.

Exosporium Link

Sporodochia convex, compact; conidiophores dark, simple, densely compacted; conidia single, oblong to cylindric, pluriseptate.

Some twenty-five species.

In part = *Coleroa* and *Coryneum*.

E. juniperinum (E.) Jacz. = *Coryneum juniperinum*.

E. laricinum Mas. is found on larch.

E. tiliaë Lk. grows on linden.

E. palmivorum Sacc. on palms.



FIG. 403.—*E. palmivorum*, 3, a sporodochium, 5, spores.
After Trelease.

Mycelia-Sterilia (p. 334)

Numerous forms are known merely as sterile mycelia. They may or may not make sclerotia. In several instances these sterile forms are so aggressive as to warrant classing them among the worst of plant pathogens. Until more is known of them it becomes necessary to arrange and name them, for convenience of reference, in a purely artificial manner.

KEY TO FORM GENERA OF **Mycelia-Sterilia**.

Tubercle-like

- | | |
|---|---------------------------------|
| Tubercles connected with fibrils..... | 1. Rhizoctonia , p. 435. |
| Tubercles without fibrils; cortex not discrete..... | 2. Sclerotium , p. 438. |
| Cobwebby or byssoid, cespitose interwoven, primary hyphæ joined in bundles..... | 3. Ozonium , p. 440. |

Rhizoctonia De Candolle

Sclerotia variable in form, horny-fleshy; cortex thin, membranous, persistent, inseparable; formed among and connected by the mycelial threads.

There are about a dozen so-called species, some of them very important plant pathogens.

The two most important species of *Rhizoctonia* may be distinguished by the following characters: *R. crocorum* appears as an external felt, pink to violet, protoplast violet, and infection

cushions present; *R. solani* has mycelium only as a web, yellow to yellow-brown, protoplast hyaline, no infection cushions.

R. solani Kühn = *Corticium vagum* (see p. 290), as does also part of what has been referred to as *R. violaceæ*.

R. crocorum (Pers.) DC.¹, ²= *R. medicaginis* DC.= *R. violacea* Tul.

The younger external hyphæ are almost colorless. As the hyphæ grow older the walls of the cells become a brownish violet which gradually deepens until the older hyphal strands are a decided violet to buff color. The young hyphal tips measure

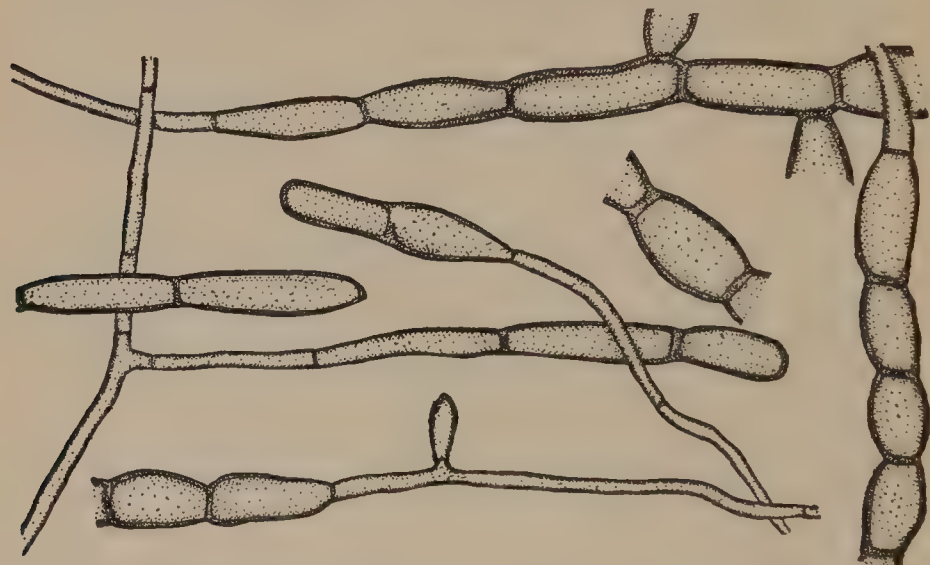


FIG. 404.—*R. crocorum*: cells characteristic of the tufted growth covering the surfaces of the large sclerotia and to a certain extent of the "infection cushions." After Duggar.

12–14 μ in diameter, while the older hyphæ measure 7.2–10 μ . The long conductive vegetative cells vary in length from 55–173 μ . The cells covering the superficial sclerotia are, as a rule, shorter, 30–50 μ , and thicker, 12–14 μ , than the cells of the conductive hyphæ. The internal mycelium strands are septate and branched, the direction of the branching here being determined by the cells of the hosts. Within the superficial mantle of mycelium on the surface of the stem there soon appear reddish-black sclerotial

¹ Faris, James A. Violet root rot (*Rhizoctonia crocorum* DC.) in the United States. *Phytop.* **11**: 412, 1921.

² Duggar, B. M. *Rhizoctonia crocorum* (Pers.) DC. and *R. Solani* Kühn (*Corticium vagum* B. & C.) With notes on other species. *Ann. Mo. Bot. Gard.* **2**: 403, 1915.

bodies. They vary from the size of a pin head to several centimeters in length, and show cells considerably branched and curiously lobed and with all varieties of color from transparent to violet. On badly infected tubers large numbers of small specks the size of a pin head, infection cushions, are to be seen; from the tops of these many hyphæ extend over the surface of the potato and young hyphal branches penetrate from them directly through the wall of a host cell and once inside branch profusely. Typical sclerotial cells are formed in the host cell until finally the cell is completely filled by the fungus. The host cells in infected tissue are disorganized until eventually several cells are broken down and

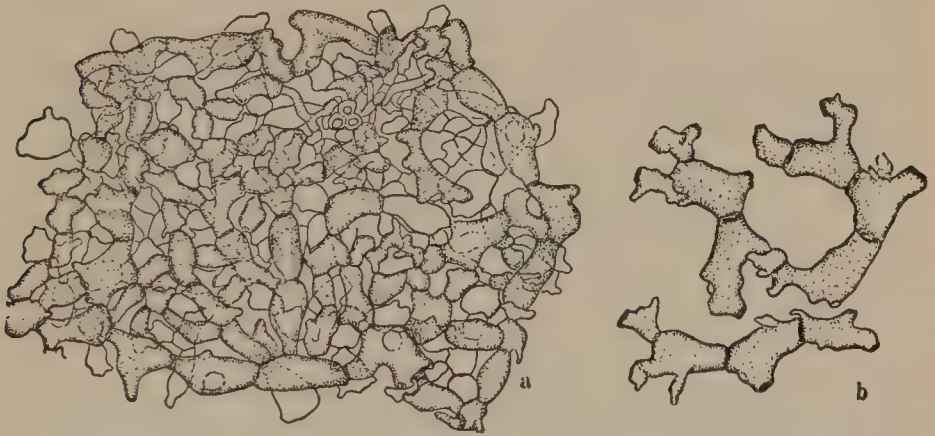


FIG. 405.—*R. crocorum*: a, extreme forms of cells isolated from a macerated sclerotium. After Duggar.

the cavities filled with a fungous mass. The infection cushions have their beginning in the cork cambium from the hyphal strands which have forced their way into the host tissue. Completely submerged sclerotia are not uncommon.

On potato, alfalfa, asparagus, carrot, beet, causing root rot; also on some 54 species in 22 families ranging from Pinaceæ to Compositæ. When abundant the fungus completely invests the root with a weft or mat of hyphæ, at first buff to violet, later red-violet to violet-brown.

On Alfalfa practically all attacked plants lose their tap roots. In heavily affected plants the cortex of the roots easily slips away from the vascular cylinder. On the potato, plants show yellowing and wilting of the lower leaves which soon drop. The entire under part of the stem is covered with mycelium. Occasionally

brown specks appeared in the epidermis of the stems and the roots; these consisting of dead surface cells of meristematic tissue, the injury not extending to the deeper layers of the cortex.

R. microsclerotia Matz.

Sclerotia superficial, small, 0.2–0.5 mm. in diameter, white when young, brown to dark brown at maturity, nearly homogenous in structure and color, subglobose, free from tufted mycelium, not smooth, usually single, sometimes conglomerated; vegetative hyphæ 6–8 μ wide, at first hyaline and granular, brown and more or less empty with maturity.

On living leaves, branches and fruit of the cultivated fig.

Others are on saffron, pine trees, coffee, buckwheat.

Sclerotium Tode (p. 435)

Sclerotia roundish or irregular in form, cartilaginous-fleshy, not connected by mycelial threads; cortex thin, membranous, inseparable.

Over 200 species have been described.

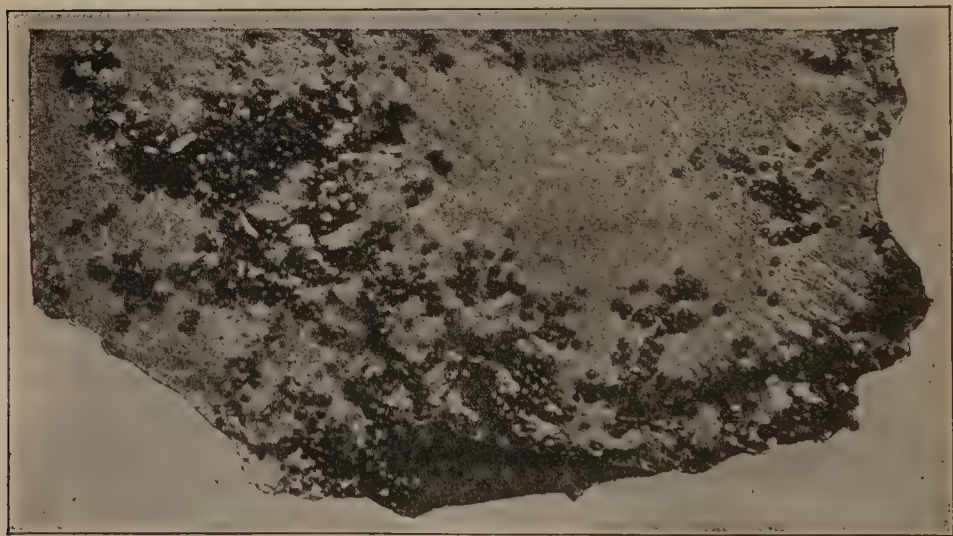


FIG. 406.—*S. rolfsii*, sclerotia. After Halsted.

S. rolfsii Sacc.

Sclerotia small, brown, about the size of a mustard seed.

This sterile fungus possesses a very aggressive mycelium which under favorable conditions of moisture grows on almost anything

living or dead, producing a dense white cottonlike mass of threads. Soon the sclerotia form as mustard-seed-like bodies. They are produced in great abundance on all media but neither these structures nor the mycelium have yet been seen to bear spores of any kind. The fungus was first studied by Halsted. It was described and named by Saccardo from specimens communicated



FIG. 407.—*S. rolfsii*, sterile mycelium growing on carrot. After Stevens and Hall.

by Stevens. Varietal strains occur as is shown by physiological and morphological differences in cultures.

S. bataticola Taub.

Sclerotia jet black, very minute; exterior smooth, made up of anastomosed, black hyphæ; interior light to dark brown, of free, thick-walled cells; sclerotia spherical, oval, oblong, elliptical, curved or even forked, varying in size from 25×22 – $152 \times 32 \mu$, abundant throughout the entire root of the host.

Parasitic on living roots of sweet potato, causing black rot.

S. oryzae Catt.

Sclerotia black, $\frac{1}{10}$ mm. in diameter, glistening, arising from a slender white mycelium. The cause of injury to rice plants.

S. rhizodes Awd.

Subglobose, at first white, villose, then smooth, black, rugose. On wheat, also on Calamagrostis and other grasses.

Other species are on tulips, onions and other bulbs.

Ozonium Link (p. 435)

Cobwebby or byssoid, cespitose, hyphæ densely interwoven, primary hyphæ fasciculate.

Some twelve species.

O. omnivorum Sh.¹

Mycelium dirty yellow, sometimes whitish when young, growing in the vascular bundles of the host; hyphæ forming strands and spreading from them, producing a rather dense arachnoid layer on the surface of the host and bearing 1 to 4 branches arising and growing at right angles from the same point near the ends, 3 to 5 μ in diameter, tapering toward the ends.

It causes root rot on almost any kind of plant including among its hosts a large variety of trees. The fungus destroys the smaller rootlets, cortex of older roots and invades the vascular system and medullary rays, resulting in wilt and death. It may be seen superficially as dirty yellowish strands or as a thin web. Sclerotia-like bodies appear on the roots often at lenticels. Inside of the host tissue the mycelium is not typically associated to form strands and its cells are hyaline.

¹ Duggar believes the conidial stage to be a *Phymatotrichum*.

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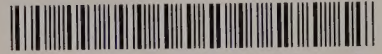
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